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Motor Learning

John W. Krakauer,^{1,2,3} Alkis M. Hadjiosif,¹ Jing Xu,^{1,3} Aaron L. Wong,^{1,4} and Adrian M. Haith^{*1}

ABSTRACT

Motor learning encompasses a wide range of phenomena, ranging from relatively low-level mechanisms for maintaining calibration of our movements, to making high-level cognitive decisions about how to act in a novel situation. We survey the major existing approaches to characterizing motor learning at both the behavioral and neural level. In particular, we critically review two long-standing paradigms used in motor learning research—adaptation and sequence learning. We discuss the extent to which these paradigms can be considered models of motor skill acquisition, defined as the incremental improvement in our ability to rapidly select and then precisely execute appropriate actions, and conclude that they fall short of doing so. We then discuss two classes of emerging research paradigms—learning of arbitrary visuomotor mappings *de novo* and learning to execute movements with improved acuity—that more effectively address the acquisition of motor skill. Future work will be needed to determine the degree to which laboratory-based studies of skill, as described in this review, will relate to true expertise, which is likely dependent on the effects of practice on multiple cognitive processes that go beyond traditional sensorimotor neural architecture. © 2019 American Physiological Society. *Compr Physiol* 9:613-663, 2019.

Didactic Synopsis

Major teaching points

- Motor learning can be defined as any experience-dependent improvement in performance.
- Explicit and implicit processes both contribute to how we learn new motor skills.
- Implicit adaptation serves to maintain motor performance in a fluctuating environment through a sensory-prediction-error-driven learning mechanism.
- Discrete sequence learning tasks reveal how we anticipate temporal regularities in the environment, but are not likely good models for skilled continuous sequential actions.
- Many skills, like riding a bicycle, cannot be assembled from pre-existing skills and require building a *de novo* controller.
- Motor acuity—the quality of movement execution—can be improved through practice.
- Implicit adaptation is dependent on the cerebellum.
- Explicit components of both adaptation and sequence tasks have been shown to have pre-frontal and hippocampal dependencies.
- Action selection is associated with interactions between the basal ganglia and motor cortex.
- Motor acuity is accompanied by changes in primary and premotor cortex, and cerebellum.

Introduction

Motor learning is a blanket term that encompasses a huge diversity of phenomena, approaches, and disciplines. It can apply to movements made by almost any animal species with any effector in any task. It is of enormous practical relevance to physical therapists, musicians, dancers, athletes, pilots, sports coaches, and animal trainers to name but a few. Motor learning is also of great theoretical and experimental interest to psychologists and neuroscientists. From a cultural standpoint, displays of motor skill arguably exert more fascination than any other form of entertainment. For example, over 1 billion people watched 22 men play with a spherical object in the 2018 World Cup Final, with more than half the world watching the tournament at some point. The reason for the worldwide obsession with expertise in throwing, kicking, and hitting balls, in hip hop dancing and ballet, and in boxing and Kung Fu remains a mystery, but the answer almost certainly relates in part to the years of practice required to perform at

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such a high level. We seem to appreciate and are impressed by the feats of learning required to become expert at a sport or with a musical instrument. How are such skills acquired?

The challenge at hand in reviewing the topic of motor learning is to bring taxonomic and conceptual order to bear on a daunting amount of seemingly loosely related phenomena that involve broad regions of the brain. Additionally, acquiring motor skills in the real world, such as becoming an expert tennis player, can take thousands of hours. However, the majority of research on motor learning focuses on more elementary forms of learning, such as adapting pointing movements while wearing displacing prisms. This adaptation process takes only minutes to reach asymptote. Are there any common principles connecting this and similarly simple forms of motor learning to the attainment of expertise in complex skills? We suggest that, although simple learning tasks may not enable us to fully understand how complex, real-world skills are learned, these tasks do provide foundational insights into components of learning that are likely necessary (if not sufficient) to account for how more impressive skills are learned (Fig. 1). These learning components can be classified into one of three primary stages along the motor planning pathway from stimulus to action (473): formation of a movement goal (332), selection of the appropriate action to achieve that goal, and execution of the selected action. Each motor learning paradigm likely drives changes at one or more of these stages, and thus

provides some insight into motor skill learning. Moreover, due to their reasonably short duration, these tasks are more amenable to rigorous examination in a laboratory setting. The focus of this review will therefore be on studies of relatively simple learning tasks in both human and non-human models with an emphasis on understanding how practice in the context of these tasks leads to changes in behavior. Much of motor learning research has attempted to identify learning principles, test computational theories, and discover physiological mechanisms (Fig. 2) supporting learning in these specific tasks. We nevertheless also hope to extract more general insights pertaining to motor skill learning.

The scope of motor learning

It seems self-evident that the essence of motor learning is about producing more effective movements. In most cases, this amounts to the process of attaining motor skill. This focus on movement is thus what distinguishes motor learning from perceptual learning or the learning of abstract concepts like the rules of Latin grammar or chess. It is likely, however, that many common principles apply across these domains. Although the boundaries around what constitutes motor learning are fuzzy, here we will exclude cases where a cognitive operation is simply *read out* by the motor system, for example moving a piece in a chess game. That said, it is important

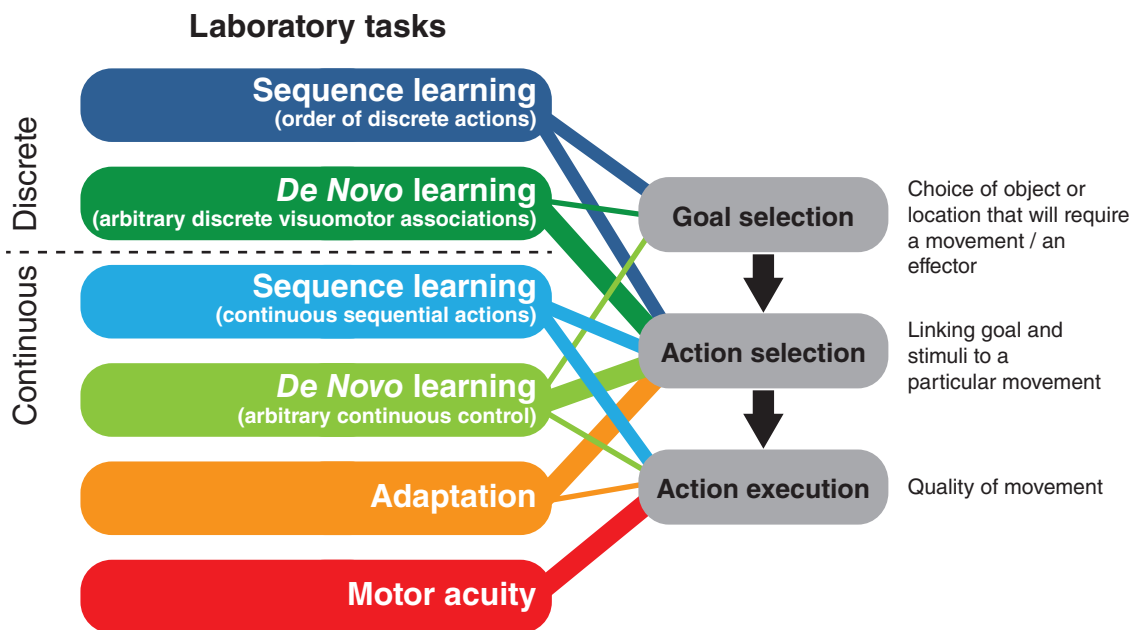


Figure 1 Motor learning tasks covered in this review and their relation to the pathway from goals to actions. Being skilled in any motor task requires effective *goal selection* (i.e. where to move to or what to act on), effective *action selection* (i.e. what movement can achieve the selected goal), and accurate and precise *action execution*. Improvements at any stage of this pathway can be described as “motor learning”. Different motor-learning tasks stress improvement at different stages of this pathway. For instance, tasks that involve discrete actions – either as part of a learned sequence or through a learned association with discrete stimuli – require improved action selection and goal selection, but do not require any improvements in action execution. Conversely, tasks that focus on learning at level of action execution (motor acuity paradigms) typically do not involve any learning at the level of goal selection or action selection. Other motor learning tasks (e.g. continuous sequence-production tasks, adaptation tasks, and tasks that require *de novo* learning of a new controller) likely engage learning at multiple levels.

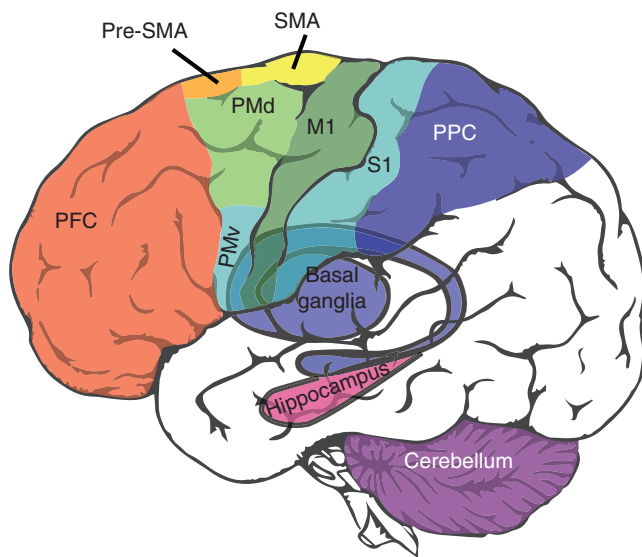


Figure 2 Brain regions that contribute to motor learning. Numerous regions throughout the brain have been identified as contributing in some way to motor learning at the level of goal-setting, selection, or execution. Discussion of the contributions of these regions to specific categories of motor learning paradigms may be found within the corresponding sections of this review. *Index to abbreviations:* PFC (red): prefrontal cortex; SMA (yellow): supplementary motor area; pre-SMA (orange): presupplementary motor area; PMd (bright green): dorsal premotor cortex; PMv (cyan): ventral premotor cortex; M1 (dark green): primary motor cortex; S1 (cyan): primary somatosensory cortex; PPC (blue): posterior parietal cortex; hippocampus (pink); cerebellum (purple); basal ganglia (blue). Note that the colors used here are not intended to relate to the colors used in Figure 1.

to emphasize, as we elaborate in the following section, that cognition is very much part of motor learning when actions need to be selected at the right time, in the right order, or in the right combination.

Most obviously, motor skill involves precise execution of movements. When a tennis player hits a topspin backhand, she must activate the right muscles at exactly the right moments to bring about the required movement with maximal precision. However, there is more to motor skill than mere execution. Typically, motor skill also involves rapid selection of the right action in the right context. What makes a tennis player choose to select a backhand over other potential shots? The answer is that she picks up on numerous sensory cues that she has learned to use to anticipate the oncoming trajectory of the ball and selects the response that is likely to have the most successful outcome given those cues. Making such decisions rapidly and accurately is an integral part of any skill. We therefore include acquiring the capacity to make these rapid decisions within our definition of motor learning. Likewise, we also consider the development of sight-reading in skilled musicians (the rapid transformation of musical symbolic notation into the correct actions) or the acquisition of touch-typing to be examples of motor learning.

Besides improving skill, motor learning also encompasses mechanisms for maintaining consistent performance in a fluctuating environment. The human body is ever changing and

prone to fatigue, growth and injury, meaning that the same motor commands will not always lead to the same movement outcomes. It is not only the body that is subject to change but also the environment. The dynamics of a tool might be altered through use, or different weather conditions might affect the trajectory of a ball. Adapting to all these ongoing changes to maintain a previously attained level of performance is also an important aspect of motor learning.

To summarize these various considerations, we adopt a two-part operational definition of *motor learning*: (i) skill acquisition—the processes by which an individual acquires the ability to rapidly identify an appropriate movement goal given a particular task context, select the correct action given a sensory stimulus and/or the current state of the body and the world, and execute that action with accuracy and precision; (ii) skill maintenance—the ability to maintain performance levels of existing skills under changing conditions. These two aspects of motor learning are each important in their own right, and they likely share overlapping neural circuitry. That said, it is also clear that the brain possesses dedicated mechanisms for skill maintenance, as we discuss in the section on adaptation.

What would not be considered motor learning under this definition? This depends on the nature of the skill being acquired. Many skills can be extremely complex and require practice over thousands of hours. In these cases, the term “expertise” becomes more appropriate than skill. Typically, expertise in complex motor tasks requires cognitive operations that go beyond sensorimotor mappings. For example, an expert tennis player may notice that her opponent is way behind the baseline and their weight is moving backward, and therefore decide to play a drop shot because she knows her opponent will not be able to get to the ball in time. An experienced musician may decide to play part of a composition at a slower tempo because he knows it will have an increased emotional effect on the audience. For the purposes of this review, we consider these two examples to fall too far on the cognitive side of tennis and musical expertise, respectively, to be considered examples of *motor* skill. Consequently, acquiring these aspects of expertise falls beyond the definition of motor learning. However, any real-world motor task necessarily entails both cognitive and movement components, and the boundary between them is often subjective.

Although we have emphasized the importance of cognitive operations in expert performance, we do not want to give the impression that cognitive operations only contribute to expertise. Rather, cognitive involvement appears to be important for acquiring almost any motor skill, even elementary ones. Thus, even though we have decided to largely sidestep the topic of motor expertise, the role of cognition will remain prominent throughout this review.

Motor skill learning versus implicit learning

It is often considered that motor learning is an implicit phenomenon, lacking any explicit cognitive contribution—contrary to our claim that explicit processes play an important

role in motor learning. Implicit learning has been tied to two separate notions. One is that “implicit” implies being unconscious or unaware (though awareness is notoriously challenging to measure (156, 392)—for example, what someone is aware of might not be apparent because the wrong question was asked or it cannot be easily verbalized). The second notion is that some process is considered to be implicit when it is non-intentional or automatic. It could be argued that both of these properties apply to an overlearned motor *skill*—one can ride a bike without needing to attend to or be aware of how we are moving our hands and feet, and the movements required to stop, start, steer, and stabilize could plausibly be described as automatic. However, these attributes should not be extrapolated to the process of motor *learning*. Even if the endpoint of learning is an implicit, procedural skill, the process of arriving at that skill is, in most cases, a richly cognitive enterprise, building on instruction, imitation, and moments of insight.

We suggest that the misconception that motor learning is purely or mainly an implicit process can be traced back to the classic findings in the amnesic patient HM (416). Specifically, HM was a patient who developed a profound anterograde amnesia after undergoing a bilateral temporal lobectomy for intractable epilepsy. After this operation, he would forget events within minutes of their occurrence. In a now classic experiment, the neuropsychologist Brenda Milner had HM perform a mirror-drawing task in which he had to trace the perimeter of a star shape with a pencil while viewing it through a mirror. The critical finding was that HM showed improvement in the mirror drawing task across 3 days even though he had no recollection, or even a sense of familiarity, of the task when he re-encountered it on days 2 and 3 (296). Since that experiment, it has largely been assumed that motor skill learning is dependent solely on procedural memory systems and not declarative memory systems. Indeed, in a famous tree diagram outlining the taxonomy of long-term memory systems, skills and habits appear on the procedural side of the tree (413). Subsequent reviews then equated procedural *memory* with implicit *learning* (414), under the assumption that, if a task can ultimately be performed without awareness, then the learning must have been implicit and was at no point dependent on explicit (declarative) processes. The study of motor learning in psychology and neuroscience has subsequently emphasized implicit learning, through the use of paradigms such as the serial reaction time task (SRTT) and adaptation tasks.

Where is the fallacy in the logic that motor learning is an implicit process? For one, the HM result demonstrates that declarative *memory* was not necessary to learn the mirror drawing skill across days, but it does not rule out that HM used declarative *processes* within each session to perform the task. Indeed, HM had to follow instructions each day about what to do in the task. More recent work has reinforced this idea, showing that the combination of instruction and implicit learning is necessary for amnesic patients to learn novel tools (364). A second reason is that explicit strategies

and knowledge can be automatized through practice (15, 152, 264) and thus become implicit. At least one of the authors of this review (JWK) can no longer recall his ATM pin number but has no problem typing it in when placed in front of the keypad. Something similar could conceivably have happened to HM within or between training sessions.

Thus, although many aspects of motor skills that we learn can eventually become implicit this does not mean they were initially learned implicitly. A recurring theme in this review is that explicit, cognitive processes contribute to almost all forms of motor learning. In many instances, particularly early in learning, explicit processes may dominate learning. As we shall discuss, even in paradigms devised to study motor learning as an implicit phenomenon (e.g., adaptation and SRTT tasks), explicit processes persistently intrude and often turn out to be in the driving seat. The notion of multiple, interacting memory systems has long influenced notions of motor skill learning (107, 461). Though such theories have been muted by the influence of the findings in HM, interactions between implicit and explicit memory and learning processes have re-emerged as a prominent theme in motor learning.

Adaptation

Motor adaptation refers to a particular type of behavioral change that involves adjusting how an already well-practiced action is executed to maintain performance in response to a change in the environment or the body, either by selecting an alternative well-practiced action or modifying how the current action is executed. In either case, the goal of the action (e.g., reach to a target) remains the same. Adaptation is thus distinguishable from *de novo* motor learning; under the latter, a new motor controller (that is, some network or process that generates motor output given the state of the body and current goals) is formed from scratch rather than derived from existing ones (we discuss *de novo* learning in a later section). For example, if an experienced tennis player picks up a new, heavier tennis racket, she is likely to adjust her existing controller, rather than assemble an entirely new one.

Aside from adjusting to a different tool, there are many other reasons why we might need to recalibrate our actions on a continuing basis. First, the dynamics of the environment are inherently variable. The dynamics of a tennis ball may be affected by changes in the wind, humidity etc. The body itself is also liable to change. A muscle can strengthen or weaken through use or with ageing. The properties of a muscle also change over very short timescales due to fatigue (99, 119). Injuries (e.g., pulling a muscle) might render some actions temporarily unavailable. In all these cases, the same motor commands issued by the brain that at one time may have led to perfect performance will now fail to do so, and therefore our existing motor controllers must be adapted to maintain performance. The need to maintain our skills in an ever-changing environment is evidently so pervasive that the motor system appears to possess a dedicated mechanism for

recalibrating our actions. The cerebellum plays a critical role in this mechanism.

Motor adaptation has been widely studied ever since Helmholtz's nineteenth-century experiments, in which participants wore prism goggles that shifted the visual field (444). Prism goggles provide a vivid illustration of the adaptation phenomenon, but their use in basic science has largely been replaced by other paradigms that afford more precise and flexible control over the types of perturbations a participant experiences. Extensive study of various adaptation paradigms has allowed the brain's mechanisms for recalibration to be characterized in considerable detail. It has become clear, as we shall discuss, that although cerebellum-dependent recalibration is an important mechanism supporting adaptation, in most cases exposure to a perturbation also engages additional learning mechanisms, such as the use of explicit cognitive strategies, which exhibit different properties from cerebellum-dependent learning. In this section, the term "adaptation" will refer to the process of reducing error in adaptation paradigms, that is, it is agnostic to underlying learning mechanisms. It is nevertheless unavoidable that this will lead to confusion on occasion, especially when giving a historical account, because many of the earlier studies in this area assumed a single mechanism was responsible for error reduction in adaptation paradigms.

Motor adaptation paradigms

Numerous approaches have been used to elicit adaptation in laboratory tasks. One common approach is to alter the dynamics of the body during movement. In reaching movements, for instance, this is often achieved by having the participants hold a robotic arm that applies forces to the hand during point-to-point reaching movements. The imposed forces usually depend on the position and/or velocity of the hand to create a "force field" in which the hand must move (389). For example, in a "viscous curl field," the imposed force is proportional to the current speed of the hand, but is directed orthogonally to the direction of movement. A similar velocity-dependent force-field perturbation can arise, even without the need for a robotic arm, when participants make reaching movements while seated on a rotating platform (255). Other dynamic perturbations can involve the addition of static loads on different positions relative to the arm's center of mass to alter intersegmental limb dynamics (250, 369). In all cases above, perturbations initially lead to movement errors but, through experience, participants learn to generate forces that can counter the imposed loads to regain their baseline levels of performance (Fig. 3).

Another popular approach is to impose a novel mapping between motion of an effector and the corresponding visual feedback. As with a force field, this initially results in unexpected errors that require the motor system to adjust future movements. Historically, such visuomotor perturbations have been accomplished by the use of prism glasses, which can displace the visual field vertically or laterally (444). Computer-based setups allow for much more direct and flexible control

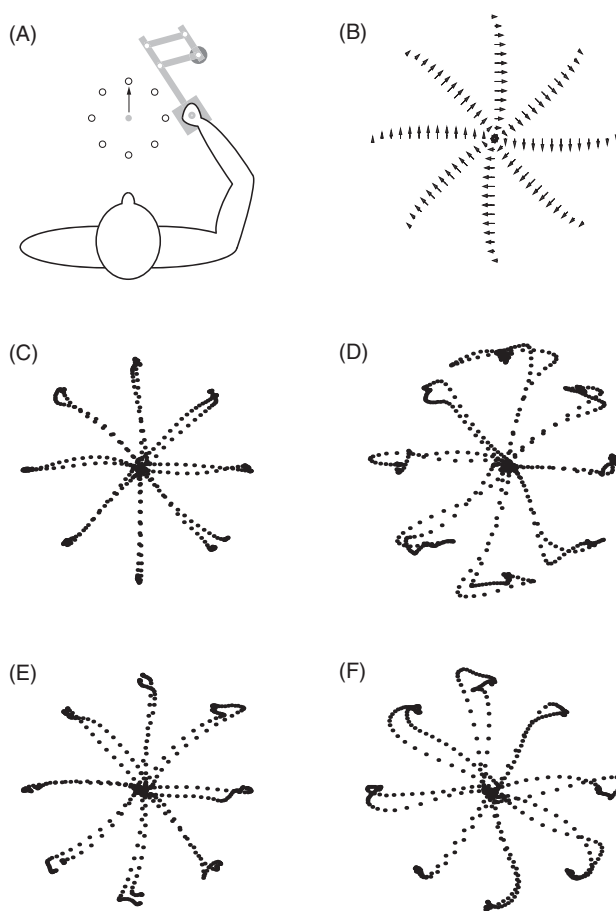


Figure 3 Force-field adaptation and aftereffects. This figure illustrates behavior in a typical force-field adaptation task (408). In this study, participants held a robotic manipulandum, illustrated in panel A, and made planar reaching movements toward eight different targets spaced 45° apart. After a baseline, unperturbed period, the manipulandum applied a force proportional to the speed of the hand, and directed perpendicularly to the direction of movement, as illustrated in panel B. Whereas baseline, unperturbed movements were relatively straight (C), the introduction of the force field resulted in movement errors in the direction of the force field (D). After prolonged training, participants adapted to the force field, resulting in straight trajectories (panel E). Interspersed with the training trials were occasional "catch" trials, in which the force-field was removed, revealing the *aftereffects* of adaptation, with movements exhibiting errors in the opposite direction to the perturbation as shown in panel F: note how the direction of errors for each target in F is opposite to those experienced in D (and opposite to the direction of the perturbation in B). Panel A is adapted, with permission, from (134); panels C to F are adapted, with permission, from (408).

of the relationship between hand position and the position of an on-screen cursor. The most commonly used visuomotor perturbation is visuomotor rotation (VMR) (253), in which cursor feedback is rotated by an angle (often around 30° to 45° , though it can be larger or smaller) about the starting position of the movement (Fig. 4). Another commonly used type of perturbation is a change in the visuomotor gain, by either amplifying or reducing the amount the cursor moves for a given displacement of the hand, just like changing the sensitivity of a mouse cursor (253, 333, 341).

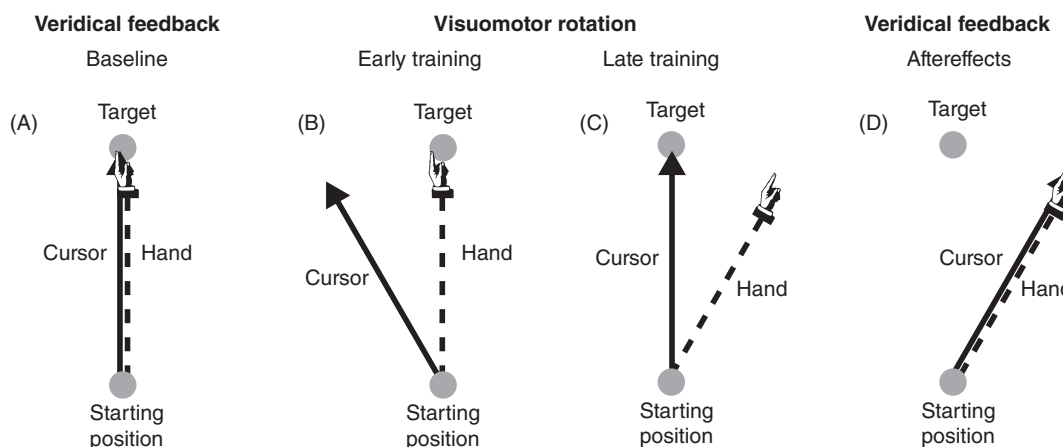


Figure 4 Visuomotor rotation adaptation. In visuomotor adaptation studies, participants typically make reaching movements without direct vision of their hand but instead observe the movement of a cursor which represents the location of their hand. During baseline, unperturbed movement, the cursor follows the hand position (veridical visual feedback, A). In B, a visuomotor rotation makes the cursor move in a direction 30° counterclockwise relative to hand motion, resulting in error. After learning, the hand moves at a 30° angle relative to the target direction bringing the cursor directly to the target (C). Removal of the rotation leads to aftereffects (D); moving along the adapted hand direction now leads to a 30° clockwise error.

Interestingly, different types of perturbations such as the above appear to be learned independently, likely because the recalibration process can operate on different kinds of error. For example, learning of novel dynamics can take place independently of learning of novel kinematics (250). Patient studies provide further evidence for this dissociation between adaptation to kinematic and dynamic perturbations. Rabe and colleagues examined deficits of patients with cerebellar damage when performing these two types of task (347) and found no correlation between them. As these patients had lesions in various parts of the cerebellum, this finding points toward the idea that different variables (in this case types of error) are processed in a similar way but by different parts of the cerebellum.

In addition to force field perturbations and visuomotor perturbations to reaching movements, there are several other commonly used motor adaptation paradigms. Adaptation can occur in relatively simple behaviors, such as altering the gain of the vestibulo-ocular reflex (216, 359). Saccadic eye movements can be adapted by displacing the target during the movement to induce an adaptive change in the gain or direction of the saccade (80, 237, 289, 476). This target-jump approach can also be used for reaching movements (269, 452). Adaptation of gait can be induced using a split-belt treadmill that can impose different speeds on each leg, which results in an adaptive adjustment of gait parameters such as step length or step symmetry to overcome asymmetric walking patterns induced by the speed mismatches (205, 271, 282, 303). Adaptation of speech production can be elicited by distorting auditory feedback of generated speech so that it sounds different (183, 331). Despite the different modalities employed in these paradigms, the goal of these experiments is similar: to examine how previously existing motor controllers are adjusted to maintain performance in the context of errors induced by a perturbation.

Basic properties of behavior in adaptation paradigms

Learning from errors

When a previously unseen perturbation is applied to movement, participants do not counter the error in a single trial. Rather, actions are adjusted little by little over a number of trials. Typically, the extent of correction from one trial to the next depends on error size. On the first trial after a large perturbation is introduced, the movement errors are large and participants generate a relatively larger correction. As learning proceeds, the errors get smaller and, consequently, so do the corrections. Assuming the perturbation applied is the same for each trial, this process results in the characteristic exponential time-course of error reduction seen almost universally in adaptation paradigms. In cases where the perturbation randomly varies from one trial to the next, the motor system adapts to the average value of the perturbation (147, 190, 374, 419).

The observation that corrections generally scale with the experienced error suggests that learning can be described in terms of a *rate*—the fraction of the error corrected from one trial to the next—that is invariant across different error sizes. For example, with a fixed learning rate of 0.5, a 1 degree error leads to an additional half a degree of adaptation in the next trial, while a 10 degree error will lead to a 5 degree adaptation. For relatively small error magnitudes this proportionality is largely true—people do correct for a fixed fraction of their error. However, it seems that the adaptive responses to perturbations tend to saturate as the size of errors becomes large (273, 447). This appears to be true regardless of the nature of the perturbation. Consequently, learning is inconsistent with a constant “rate” parameter, but instead could be described in terms of a learning rule in which the rate (or “sensitivity”)

decreases with increasing error size. Alternatively, it has been suggested that declining error sensitivity may not be the best way to view this saturation; instead, it may reflect a limitation in the amount of error that can be corrected from one trial to the next (228).

Regardless of the nature of the learning rate, why doesn't the motor system correct the entirety of the error in a single step? One might assume that this is due to limitations in underlying plasticity mechanisms required to implement the update. However, this explanation seems implausible. If a large correction can be generated for large errors, why can't a small error be corrected completely? Furthermore, difficulty in forming a new motor plan could plausibly apply in the case of force field learning, but not for visuomotor rotation, where the adapted movement to a visuomotor rotation is simply a regular reach aimed in a different direction from the displayed target.

An alternative explanation is that the incremental nature of adaptation reflects a rational response to the observed error. Noise in issuing the desired motor command, and uncertainty associated with observing the error mean that not all of the perceived error should necessarily be corrected. In the extreme case, if the error were solely due to noise, it would be inappropriate to correct for it at all. Hence, incomplete learning from one trial to the next could be a consequence of uncertainty about what compensation would be required on the next trial. This view formally corresponds to a Bayesian perspective of learning (244), according to which adaptation is essentially a problem of estimating the properties of the imposed perturbation given both the noise in the motor system and the likelihood that the environment itself may be changing.

Retention and De-adaptation

We have described motor adaptation as a process that occurs by adjusting an existing controller to maintain performance levels under new circumstances, rather than creating a brand new controller. This assertion stems from a ubiquitous signature of motor adaptation: the presence of aftereffects after the perturbation is removed. For example, if a participant has learned to produce a leftward force to counter a rightward force-field, abruptly removing the force-field on the next trial will cause the hand to deviate toward the left, as the participant generated a leftward force in anticipation of a rightward perturbation that is no longer there. Importantly, these aftereffects can be involuntary. They occur even when the participant is fully aware that the perturbation has been removed (235, 353, 421). Thus adaptation to a perturbation is, at least in part, an implicit process.

However, this aftereffect appears to be inherently transient. The adapted state of the motor system rapidly reverts to baseline on subsequent trials in the absence of a perturbation (146, 190, 232). Extinguishing adaptation in this way is commonly referred to as *washout* and occurs quite rapidly (Fig. 5)—usually slightly faster than the rate of adaptation

to the perturbation in the first place. This washout is in part driven by the same error-based process that operates during acquisition, except that the observed errors are now in the opposite direction. However, washout is also abetted by an additional tendency for behavior to revert or “decay” toward baseline.

This decay of adaptation can be most clearly seen when participants continue to move but are not provided with meaningful observed errors. This can be accomplished in one of two ways. First, by removal of relevant sensory feedback—for example, by hiding the cursor during visuomotor adaptation (117, 232). An alternative approach is to manipulate sensory feedback so that experienced errors are minimized and performance appears essentially perfect regardless of the true motor output. This approach is often referred to as an “error clamp,” since observed errors are “clamped” to be zero. In visuomotor adaptation, an error clamp can be accomplished by simply projecting visual feedback of the hand position onto a straight line passing through the target (232, 437). In force-field adaptation, an error clamp can be achieved by mechanically constraining the hand to move along a straight line toward the target (49, 375, 436). In either case—whether sensory feedback is removed altogether or manipulated to give the impression of minimal error—there is a similar gradual, roughly exponential decline in adapted state over time (Fig. 5).

Besides decaying when moving in the absence of errors, motor adaptation can also decay passively with the passage of time in the absence of any movement (70, 146, 232, 403). For example, simply waiting for about 12 min (approximately the time required to complete the washout block) reduced the extent of compensation by roughly 50% (232). Adaptation does not, however, appear to decay completely with time, as discussed in more detail in the later section on temporally stable versus temporally labile adaptation.

The reason for the decay of adaptation remains unclear. However, the fact that adaptation does spontaneously and rapidly revert to baseline clearly demonstrates that it is a temporary adjustment to the existing baseline controller, rather than the formation of a new controller. The transient and reversible character of adaptation provides a stark contrast to motor skill learning, which is characterized by slow learning over months or even years but tends to be long-lasting. This difference casts serious doubt on whether adaptation can serve as a good model for motor skill learning.

It is important to note, however, that although adaptation seems to be short-lived, under certain conditions it can exert a longer-term influence on behavior. In the absence of active washout, some aftereffects of adaptation have been observed to persist, albeit fractionally, over 24 hours, in visuomotor (104, 249, 250, 459), force-field (70, 215), and saccadic adaptation (7). Furthermore, even when such aftereffects do not occur or have disappeared, the memory of the adapted state does not seem to be altogether eradicated; when participants experience the same perturbation a second time, they adapt to it faster (a phenomenon typically referred to as *savings*). The existence of savings demonstrates that there is a long-term

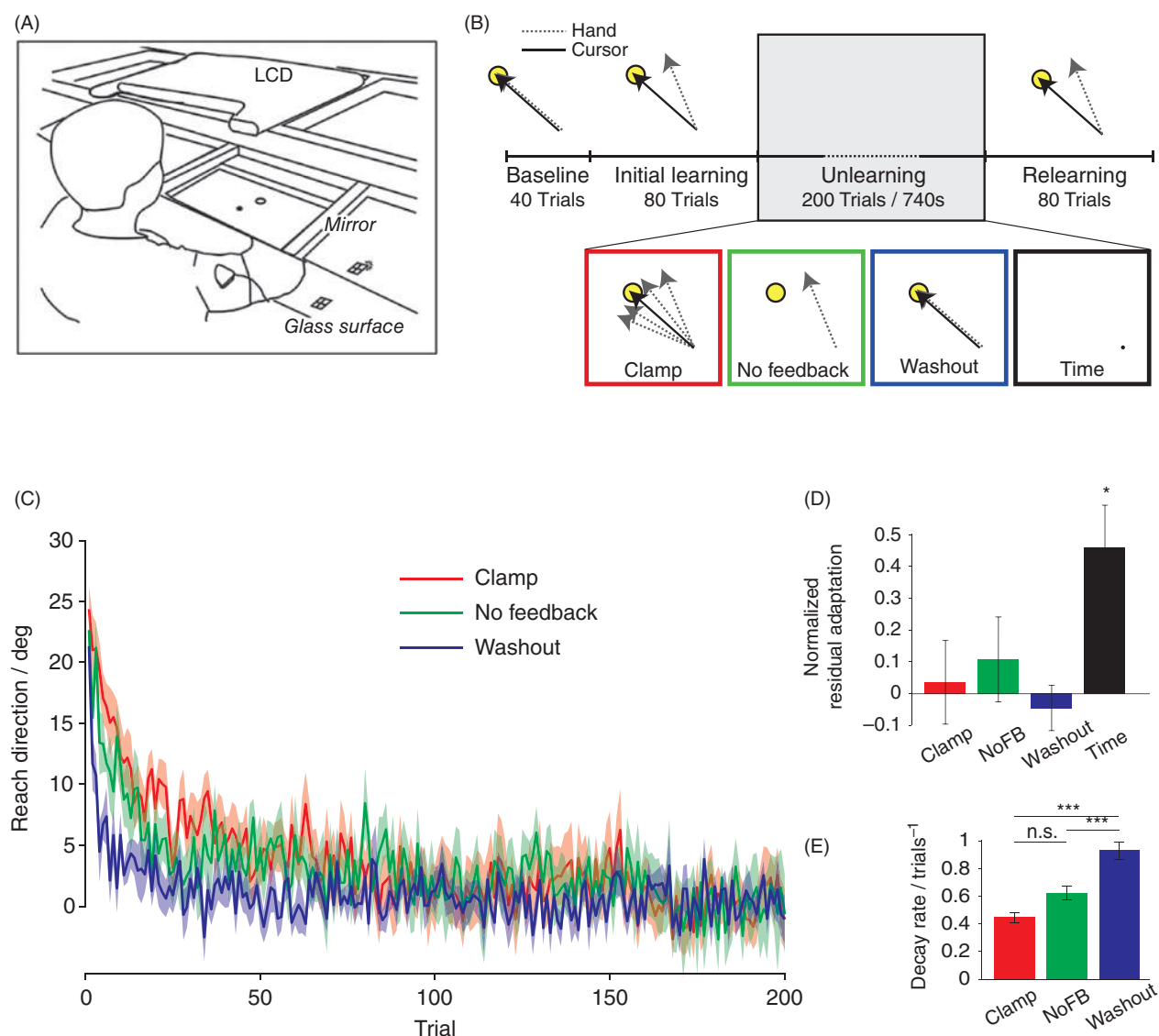


Figure 5 Forms of deadaptation. Panels are taken from a study (232) that trained participants on a 30° visuomotor rotation and then subjected them to different modes of deadaptation. A shows the experimental apparatus used. B illustrates the training schedule and the four different modes of deadaptation employed: clamped feedback in red (participants' movement is projected onto a straight line connecting the start position and the target, leading to the impression of zero error); no feedback in green; washout in blue (participants receive veridical feedback); and time in black (participants do nothing for about 12 minutes—the time it normally takes to complete one of the other deadaptation blocks). The results, shown in C, illustrate considerably faster deadaptation in the washout condition compared to the clamp and no-feedback conditions. This is quantified in E, which estimates the deadaptation (*unlearning*) rate for each condition: washout deadapts at a significantly faster rate. This is not surprising: the clamp and no-feedback conditions remove error feedback, letting the adapted state slowly revert back to baseline; the washout condition, on top of that, provides an error which actively drives the adapted state back to baseline. At the end of the unlearning block, these three conditions lead to deadaptation as shown in panel D. Allowing for time to pass (black) also results in deadaptation, albeit only partial.

memory associated with the initial episode of adaptation. We will discuss savings in much greater detail in the later section on savings.

Generalization of motor adaptation

The degree to which motor learning can be expressed in conditions different than those in which it originally occurred is commonly referred to as *transfer* or *generalization*. In the case of motor skill acquisition, for instance, it is important

that skill learning can generalize from practice conditions to performance conditions. Studying generalization of learning can provide insights into the neural representations underlying learning: if learning generalizes from one condition to another, this hints at a shared neural representation for the two conditions (For a review, see (385)).

In the case of adaptation, generalization is typically assessed by comparing the extent of adaptation in the trained movement direction to that in other, untrained directions in the workspace. The extent of generalization to different directions

appears to depend on the type of perturbation applied, but this could be because of the contamination effects by other learning processes in adaptation paradigms (we discuss this in more detail later in the section on interference). Typically, the after-effects of motor adaptation are fairly local to the trained direction, corresponding to a narrow generalization pattern that falls off as a function of angular distance away from the trained direction, reaching zero or close to zero at around 45° to 60° away from the trained direction (48, 57, 85, 253, 429); this pattern of generalization is most frequently observed following adaptation to force-fields and visuomotor rotations. In contrast, gain perturbations induce a wider generalization pattern that tends to be flat across the whole workspace of different untrained movement directions (253, 341). However, gain generalization patterns still exhibit a peak around the trained direction (333). It is possible to simultaneously train different gains on different targets across the workspace, suggesting that this generalization pattern is flexible (333).

It is also interesting to consider how learning generalizes across different limb postures. This can reveal whether the underlying learning is represented in terms of an extrinsic coordinate frame (i.e., movements of the cursor in space) or an intrinsic coordinate frame (i.e., changes in joint angles). Changing the arm posture at the start of movement can dissociate these two scenarios since the same extrinsic movements (cursor displacements) now correspond to different intrinsic movements (joint angle displacements). Such approaches have largely suggested that visuomotor adaptation occurs in an extrinsic coordinate frame (253), while force field adaptation is more intrinsic (388, 389). Recent studies have, however, found evidence for the concurrent involvement of multiple reference frames—intrinsic and extrinsic, as above, but also object-centered—in adaptation to visuomotor and force perturbations (35, 48), suggesting a mixed representation that is not yet clearly understood.

Besides movement direction, generalization of motor adaptation has also been examined across different perturbation types (404), different viewing conditions (61), different movement speeds (213) or amplitudes (135, 281), and different effectors (36, 69, 155, 214, 252, 425). As stated above for gain generalization, however, some caution is required as the degree to which generalization reflects properties of implicit recalibration versus other learning processes is not always easy to experimentally disambiguate. Indeed, generalization across contexts is one area where cognitive elements are likely to play a critical role.

State-space models of adaptation

The properties of adaptation described above occur in almost any adaptation paradigm, and are largely consistent across different participants. This regularity has prompted theorists to derive a mathematical characterization of behavior in adaptation paradigms. Basic properties of adaptation are remarkably well described by a relatively simple class of models, termed *state-space models* (60, 85, 429).

In the simplest version of such a model, the trial-to-trial change in behavior during adaptation can be captured through the following equation:

$$x(k) = Ax(k-1) - Be(k-1), \quad (1)$$

where $x(k)$ represents the extent of adaptation on trial k . For example, x represents the direction of a reaching movement in a visuomotor rotation paradigm or the amount of force generated perpendicular to the direction of movement in a force-field paradigm. We assume here that behavior at baseline corresponds to setting $x = 0$, that is, no adaptation. The term $e(k-1)$ represents the error of the movement on the previous trial ($k-1$), while the parameter B represents the learning rate (or error sensitivity)—the proportion of an observed error that will be compensated for on the next trial. B has been estimated from data to typically be in the range of 0.1 to 0.3 (134, 407). This equation thus encapsulates the idea of a fixed sensitivity to error, and predicts exponential learning curves when a fixed perturbation is imposed. The final parameter, A , is a retention factor that represents the tendency for the applied compensation, x , to decay back to baseline levels ($x = 0$) with each movement. Setting $A = 1$ corresponds to perfect retention, while values of A close to but less than 1 imply a partial decline in the adapted response toward baseline from one trial to the next, as is known to occur when errors are artificially clamped at zero (232, 375, 436). Including A in this equation also accounts for the fact that deadadaptation during simple decay (e.g., where visual feedback is removed) is slower than active washout when the perturbation is removed (232). It also accounts for the well-established fact that adaptation never quite reaches full compensation for the perturbation (240, 437). Specifically, late in adaptation the opposing drives of learning from errors (B) and decay of the adapted response toward baseline (A) will reach an equilibrium at a level somewhere short of perfect compensation.

Equation 1 illustrates a simple instance of a state-space model (60, 85, 429). The basic model presented here can be extended in various ways, for instance to include compensation in different directions (85), and to include multiple components underlying the adaptive response (243, 407).

It should be emphasized, however, that these models are not intended to provide a mechanistic explanation of adaptation—they do not explain *why* adaptation has the properties it does. They explain neither why compensation for a perturbation decays, nor why people learn at the rate they do. However, these models do encapsulate a set of simple assumptions about how learning might occur on a single-trial timescale, and allow us to predict behavior in response to sustained or fluctuating perturbations over many trials. At this, they appear to do a remarkably good job (85, 429, 437).

Bayesian theories of learning provide a potential explanation as to why state-space models have proven so effective. As we described earlier, a longstanding theory in motor adaptation holds that partial learning from one trial to the next arises due to uncertainty about what compensation would be

required on the next trial (244). This theory holds that adaptation is essentially a problem of estimating the properties of the imposed perturbation, given uncertainty about sensory feedback and the state of the world. Mathematically, under certain assumptions (that the noise/variability is Gaussian in both cases), this Bayesian estimation framework becomes equivalent to a Kalman filter (219)—a common algorithm for optimally tracking dynamic states under noisy observations—which is almost identical to a state-space model.

The Bayesian perspective generates a number of additional insights besides simply accounting for learning rates. For example, if the uncertainty associated with sensory input increases, the motor system should assume that observed errors are the result of this higher sensory noise (to which adaptation would be inappropriate) instead of actual changes in the external environment (to which adaptation would be necessary). As a result, the motor system would adapt less to a given error, reducing its learning rate. This prediction has been validated experimentally (53, 447). This basic Bayesian approach has also been extended to include multiple timescales of adaptation (243), and learning across multiple contexts (252) and in multiple modalities (148). Bayesian theories have also been proposed to explain why error sensitivity declines for larger errors: if one assumes that very large errors are likely to be one-off outliers that are unlikely to recur, then it makes sense to correct relatively less for them compared to smaller errors, which are more likely to reflect a persistent change (447).

Multiple components of motor adaptation

The simple theory presented above frames adaptation as a single process that can be characterized by a simple learning

rule. This theory can capture many of the salient phenomena present in adaptation paradigms. However, numerous lines of evidence now demonstrate that adaptation is in fact supported by multiple, qualitatively distinct processes that operate in parallel (193). These observations have revealed that there is far more to how participants compensate for an imposed perturbation than just implicit recalibration of a pre-existing motor controller. Instead, multiple, qualitatively different processes occur during adaptation tasks; for example, processes driven by explicit, cognitive strategies. When it comes to studying implicit recalibration, these other processes can be a contaminant. At the same time, however, these additional processes likely reflect the involvement of similar mechanisms to those responsible for more general motor skill learning.

The first clue that multiple processes contribute to learning in adaptation paradigms is that close inspection of learning curves typically reveals two distinct time constants: fast initial learning, followed by slower, more gradual improvements later on (e.g., the red curves on Fig. 6). This two-timescale learning curve can be modeled by extending the state space model above to include *two* underlying components of learning: a “fast” process that has a high learning rate but decays rapidly, and a “slow” process that learns more slowly but has greater retention (407). The total compensation in a given trial is simply the sum of these two components. Indeed, a multiple-component model is capable of fitting a host of behavioral phenomena such as spontaneous recovery, in which, after washing out the adapted response, some fraction of that learned behavior becomes reinstated. The presence of two learning components can account for this phenomenon in situations where the sum of the two states, neither of which is at baseline, is nevertheless equal to zero (101, 407). A two-component model can also account for savings in certain

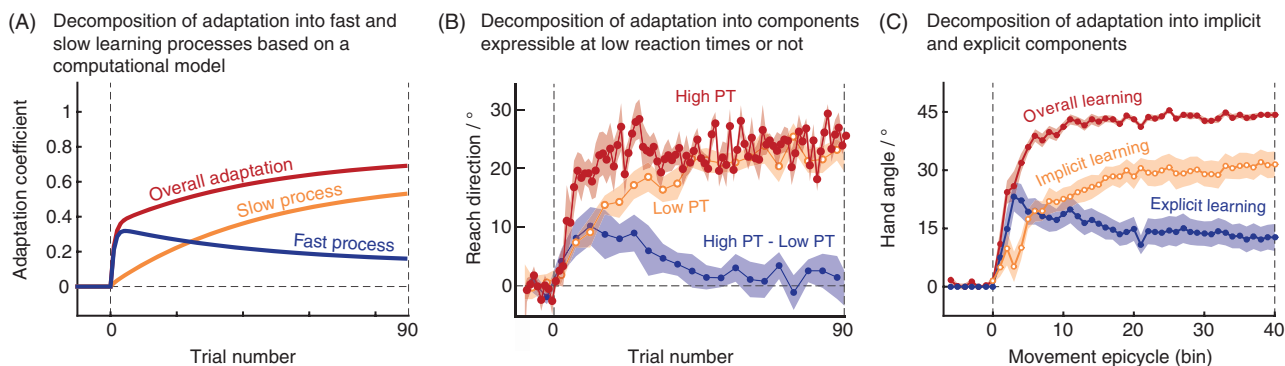


Figure 6 Multiple components of motor adaptation. It has come to be appreciated that motor adaptation is not a monolithic process but instead consists of multiple components. There are multiple different ways in which adaptation can be dissected into its component processes. These panels illustrate how each component responds after the introduction of a perturbation. (A) Using model fits, adaptation can be divided into a fast process, which learns quickly from error but has weak retention, and a slow process, which learns slowly but has strong retention [the simulation shown in this panel uses the parameter values for these two processes as found in (407)]. When a perturbation is first introduced, the fast process compensates rapidly. However, as learning proceeds, the slow process begins to compensate in addition, ultimately accounting for the bulk of learning as the contribution from the fast process diminishes. An adaptation coefficient of 1 indicates complete adaptation. (B) Decomposition of adaptation based on whether it can be expressed at low reaction time (149). In this study, participants adapted to a 30° visuomotor rotation. In a subset of trials (Low PT) participants were forced to initiate movement with a very low preparation time (~300 ms), unlike the majority of trials where they were allowed 1.5 s to prepare their movement (High PT trials). (C) Dissection of adaptation into an explicit and implicit component. Figure plotted using adaptation data from (423). In this study, participants adapted to a 45° visuomotor rotation. To assess explicit adaptation, participants were asked to report their aiming location. Implicit adaptation was then taken as equal to the difference between the aiming direction and the hand angle.

circumstances (407) (though subsequent work (487) showed that the two-state model cannot account for savings in most situations of interest), as well as other phenomena such as anterograde interference (215, 405), and the effect of inter-trial intervals on learning (403).

However, it is unlikely that the underlying components that contribute to learning in adaptation paradigms only differ in terms of their learning and retention rates, as the two-state model suggests. The multiple components of learning instead correspond to entirely distinct learning processes that are simultaneously brought to bear on the same problem. For example, it has since been suggested that the fast and slow processes can be equated to distinct explicit and implicit learning processes, respectively (286). Below we will identify and describe the nature of these component processes that contribute to performance in adaptation paradigms.

Explicit versus implicit adaptation

The most prominent way in which the components of adaptation have been dissociated is in terms of how much they rely on overt cognitive processes. This was first recognized in prism adaptation, where it was noted that aftereffects after removal of the prisms never fully match the imposed perturbation. It

was suggested that participants must therefore compensate for prism-induced perturbations, in part, through a deliberate strategy that can easily be disengaged when the prisms are removed (353). This explicit mechanism has been shown to have considerable influence in adaptation paradigms, and may even dominate learning in many circumstances (422). Providing instructions about how to deal with a perturbation results in faster adaptation for both visuomotor rotation (33) and split-belt treadmill perturbations (270). Moreover, when a strategy is not provided, participants who are able to describe the preceding perturbation accurately at the end of visuomotor adaptation often prove to have adapted better than participants whose descriptions are vague or incorrect (451).

Visuomotor rotation tasks are particularly amenable to studying the implicit and explicit components of learning because an explicit strategy presumably involves simply aiming toward a different location than the target. This was first addressed in an experiment by Mazzoni and Krakauer (285) (Fig. 7B). After two trials of experience with a 45° rotation, participants were told the exact nature of the perturbation and that they could counter it by aiming to a neighboring target 45° in the opposite direction. Following these instructions, subjects were immediately able to move the cursor directly toward the intended target. However, as they continued to aim

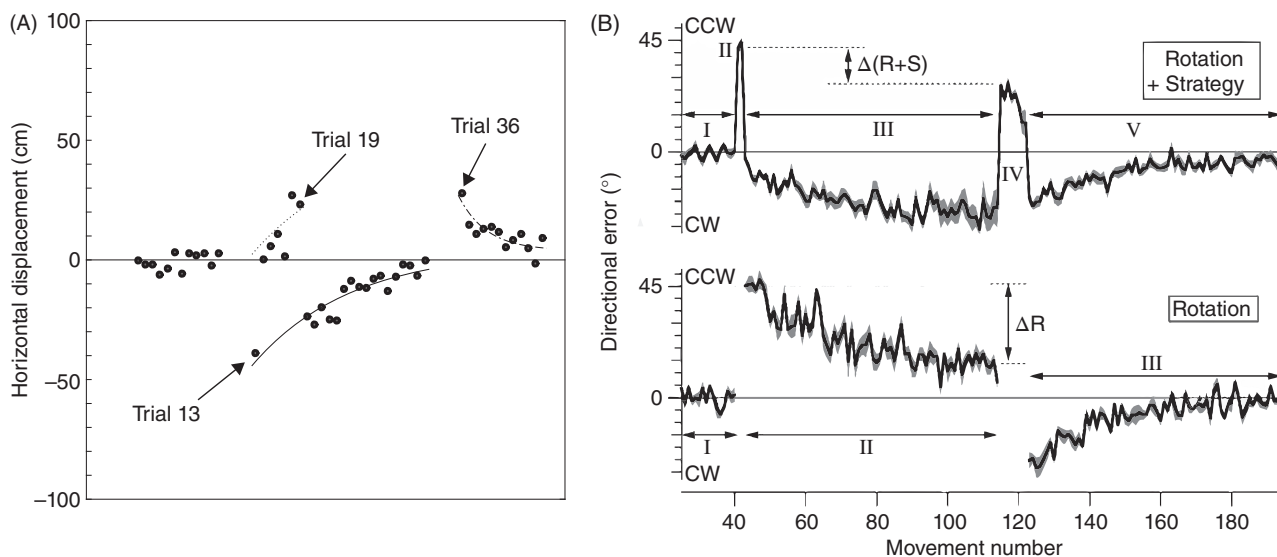


Figure 7 Implicit adaptation is involuntary and driven by sensory prediction error. (A) In this study (276), participants threw darts while looking through prisms which displaced their visual field, leading to errors. This panel shows data from one participant. After donning prism glasses (on trial 13) this particular subject utilized an aiming strategy which led to almost eliminating the error in the next trial. However, continuing to use the same strategy led to involuntary adaptation: while the strategy eliminated task error, sensory prediction errors continued to (involuntarily) recalibrate their throwing, as witnessed by the increasing error after trial 13. On trial 19, the subject was instructed to stop using their strategy and aim directly at the target. Figure re-plotted from (276); used by permission of Oxford University Press. (B) Mazzoni and Krakauer trained participants in a 45° visuomotor rotation task (285). Top panel: Experiencing the rotation for two movements (II) led to an increase of about 45° in directional error (y-axis). At that point, participants in this group were briefed on the nature of the perturbation and provided with a strategy to counter it: aim to a target 45° away on the other direction. This led to an immediate reduction in error close to zero (beginning of III). However, as participants continued to use this strategy, they began to display errors in the opposite direction due to involuntary adaptation as in A. When the participants were instructed to stop using the strategy and instead aim at the intended target (IV), they experienced errors that were significantly smaller than the 45° error that would be expected had there been no recalibration. After the perturbation was removed, participants displayed persistent, slowly decaying aftereffects (V), a hallmark of implicit adaptation. Bottom panel: participants in a further group were not provided with a strategy, but still displayed similar levels of implicit adaptation and aftereffects as the first group.

at the neighboring target, their performance worsened as their movements began to drift away from the target, exacerbating their initial instructed compensation for the rotation. The interpretation is that although participants experienced zero *task error* due to their use of the instructed strategy, the mismatch between the intended direction of the unobserved hand movement and the observed direction of the cursor movement (which represents the hand), that is, *sensory prediction error*, continued to drive implicit recalibration. This result vividly illustrates the existence of implicit adaptation and its involuntary nature. The same drift phenomenon has also been observed when participants spontaneously adopt an aiming strategy while wearing prism goggles (276) (Fig. 7) and has since been widely reproduced (382, 421).

Many experiments have since extended the original Mazzone and Krakauer result. In particular, it has been shown that, even when participants are not provided with a re-aiming strategy, they nevertheless seem to adopt one spontaneously (33, 287, 301). One way to measure the extent of re-aiming is to simply ask participants to disengage any strategy they may be applying and instead try to move directly to the target (33, 301, 320, 450). An alternative approach is to have participants report where they were aiming prior to each movement (424). The reported aiming direction relative to the target provides a measure of explicit adaptation, whereas the direction of hand movement relative to the aiming direction provides a measure of implicit adaptation. This direct-report approach has the added benefit of yielding a trial-by-trial decomposition of learning into implicit and explicit components (for example, see Fig. 6B). Tracking these contributions throughout the course of learning reveals that explicit contributions are larger in amplitude early in learning, and then persist as smaller adjustments to ongoing implicit learning (424). This illustrates the flexibility of the explicit learning component, with participants able to adjust their re-aiming strategies depending on the extent of adaptation by the implicit system (421). The explicit compensation process has been likened to mental rotation (13, 105, 288). For instance, Anguera and colleagues found that performance on a mental rotation task correlated with the rate of early, but not late, learning of a visuomotor rotation; moreover, brain activity during a mental rotation task—mapped using fMRI—was similar to brain activity during early, but not late adaptation (13).

A perhaps surprising finding emerging from this line of work is that the maximum amount of implicit adaptation to a visuomotor rotation is only around 15° to 25°, and seems to be independent of the perturbation size (44, 302). Thus, adaptation to anything more than a modest perturbation will require explicit contributions to achieve full compensation.

Another, related way to decompose learning into multiple components is to limit reaction times. Fernandez-Ruiz and colleagues (105) found that limiting reaction time during adaptation to a visuomotor rotation significantly slowed learning, and suggested that this was due to short preparation times prohibiting the use of cognitive strategies. Haith and

colleagues (149) extended this idea by limiting preparation time in only a subset of trials. Although participants adapted normally, they were only able to express a fraction of their learning in trials in which preparation time was limited, at least during early adaptation (Fig. 6C). Thus, limiting preparation time isolates a single learning process, which is likely related to the implicit process measured through explicit aiming reports (259).

One discrepancy between these two approaches (limiting preparation time versus gathering explicit aiming reports) is that, after enough trials under the perturbation, participants can compensate almost perfectly for the perturbation even when preparation time is restricted (149) whereas, with aiming reports, implicit learning never fully accounts for the net adapted behavior (424). A potential reconciliation is that the specifics of the task itself might promote one type of adaptation over the other. For example, participants are more likely to utilize explicit adaptation when they are given explicit instructions, when the visuomotor perturbation is introduced abruptly rather than gradually, when they have continuous cursor feedback (rather than only at the endpoint), and when cues and markers facilitating reaiming are present in the workspace. Alternatively, it may become possible through repetition and/or practice, to implement a reaiming strategy more automatically, avoiding the need for time-consuming computations each time (194). The nature of compensation and ability to compensate at low preparation times also appears to depend on the number of targets in the task (288).

Adaptive changes driven by sensory-prediction errors versus task errors and reward prediction errors

In principle, learning in adaptation tasks could be driven by a number of different error signals. Most obvious is *task error*, that is, the extent to which the actual movement outcome deviates from the movement goal. As we have already discussed, implicit adaptation is not in fact driven by task error but is instead driven by *sensory prediction errors*. To recap, this has been clearly demonstrated in experiments in which participants are provided instructions as to how to counter the perturbation, ensuring they achieve zero task error, while still experiencing sensory prediction errors (285, 421). An alternative approach to demonstrating the importance of sensory prediction error is to render the effects of the perturbation irrelevant to task success (302, 373). In either case, implicit adaptation occurs regardless of the lack of task error.

Another example where task errors and sensory prediction errors can be dissociated is in saccade adaptation. Saccadic eye movements tend to be hypometric, that is, they fall short of their target, requiring a secondary, corrective saccade. Thus saccades ordinarily elicit task errors but not, presumably, sensory prediction errors. Indeed, if the target of the saccade is shifted mid-movement to eliminate task error, participants

exhibit an adaptive response owing to the sensory prediction error introduced by the target jump (169,360,475).

Although implicit adaptation is driven by sensory-prediction errors, explicit compensation seems to be driven by overall task error, that is, the discrepancy between the cursor and a target (421). In addition to task errors, which provide information about direction and magnitude of an error, it is also possible that learning might be driven by simple success or failure of a movement. In many instances, it may be obvious that an error occurred but it might not be clear exactly what the direction or magnitude of the mistake was. For instance, when attempting to whistle, if you fail to make any sound at first, there is no way of knowing how you should adjust your lips and tongue to whistle successfully. In these instances, a more simple scalar error signal reporting the success or failure of the movement can still be used to guide learning. Indeed the field of reinforcement learning is devoted to this very problem (418). In motor learning tasks, by analogy with reinforcement learning, such scalar errors are often referred to as *reward prediction errors*, suggestive of the fact that, in adaptation tasks, the participant would presumably predict their baseline movement to have been successful (rewarding).

Reinforcement has been shown to influence learning in adaptation paradigms. Reinforcement of an adapted movement with binary success/fail feedback after a period of adaptation was shown to greatly enhance retention of that adaptation when visual feedback of the cursor (and thus task error feedback) was removed (397). In another study, feedback in the form of punishment (monetary loss for low performance) accelerated adaptation but resulted in reduced retention, whereas feedback in the form of reward (monetary gain for high performance) did not accelerate adaptation but resulted in increased retention (116). Although it is tempting to conclude that reward and punishment have an influence on cerebellar-dependent implicit adaptation, subsequent experimental evidence has suggested that reward and punishment effects are instead operating on the explicit process. Indeed, the implicit adaptation process appears to be indifferent to reward (56,179,241). Thus, our understanding of sensitivity to reward has followed a similar pattern to many other phenomena in adaptation paradigms—initially thought to reflect properties of implicit recalibration (e.g., savings, interference), but then subsequently found to stem from explicit compensation processes.

Learning from reward prediction errors can be studied in isolation by eliminating sensory-prediction-error based recalibration, usually by withholding continuous cursor feedback altogether during movement and instead providing a binary hit/miss or scalar score signal at the end of the movement. Using these kinds of feedback it is possible to elicit adaptive changes in movement direction, which persist after feedback is removed (201,321,397,428). However, such learning leads to narrower generalization and negligible aftereffects, compared to implicit adaptation driven by sensory-prediction errors (201).

Temporally stable vs. temporally labile adaptation

Another empirical way to decompose adaptation is through studies that systematically probe the decay of motor adaptation with time. It has long been established that varying the time interval between trials can affect how participants adapt to a perturbation (191,230). More detailed examination of this effect has shown that learning in both visuomotor rotation and force-field adaptation tasks can be decomposed into two distinct components according to their sensitivity to the passage of time: a temporally labile component that decays rapidly with time (with a time constant of about 15–20 s), accounting for 20% to 25% of overall adaptation, and a temporally stable component that does not decay with time (at least over the timescales examined, 2–20 min), accounting for 75% to 80% of overall adaptation (145,403). It seems likely that the two processes identified this way are also related to explicit and implicit learning: the stable component may correspond to implicit recalibration, while the unstable component may correspond to disengagement of explicit compensation. The exact relationship has yet to be rigorously established, however.

Adaptation, therefore, can be implicit or explicit (424). Some components of adaptation require longer reaction times to be expressed (149). Some components are fast to adapt, while some are slow (407), and can be either stable with the passage of time or rapidly decay with it (145,403). It seems likely that these various dichotomies are simply different ways of looking at the same two fundamental adaptation components: a component that learns slowly, is retained well, is implicit and expressible at low reaction times, is temporally stable, and is driven by sensory-prediction error; and a second component that learns quickly, is poorly retained, is explicit and expressible only at high reaction times, is temporally labile, and is driven by reward and task success (193).

Forward and inverse models

Implicit adaptation has been closely tied to the concept of forward models (26,193). *Forward models* are networks in the brain that predict the sensory consequences of a given motor command in a given environment (294,472) (Fig. 8). Forward models play an important role in the control of movement by allowing the motor system to counter the effects of delays in sensorimotor loops. However, a forward model predicting the consequences of a motor command could also potentially be used to plan which motor command to select to achieve a desired outcome, although there is little evidence at present that forward models are ever used in this way.

Theory suggests that learning of a forward model, as a form of supervised learning, should be guided by the errors in its output. The output of a forward model is a prediction about the sensory consequences of a movement, and thus the appropriate error signal to update a forward model is a *sensory prediction error*: the difference between where you

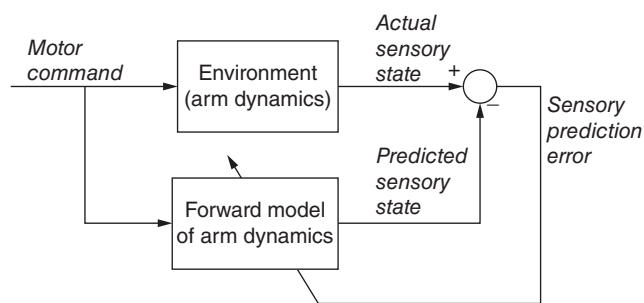


Figure 8 A forward model for the prediction of the sensory consequences of motor commands (in this case, for arm movements). In this diagram, the forward model receives a copy of the efferent motor command and predicts the sensory consequences of that motor command. If the actual sensory consequence is different than the one predicted, the resulting sensory prediction error will act as a training signal to update the forward model.

predict you will see your hand (or a cursor) and where you actually see it at the end of the movement. Modification of the forward model in this manner enables the state of the body to be more accurately estimated during movement and, in principle, could influence how we adjust future movements.

It has also been suggested, however, that errors might be used to more directly modify our controller. In this sense, the controller is often referred to as an *inverse model*, since it maps desired outcomes to motor output, the inverse of the mapping implemented by the motor apparatus. An appropriate signal to update the inverse model is the *motor error*, that is, how wrong our motor commands (the output of the inverse model) were. Unlike sensory prediction error, which is immediately available by comparing predicted outcomes (the output of a forward model) to actual outcomes, motor error is not immediately observable. Instead, motor error must be estimated from task error—a process that requires assumptions about how variations in motor output will affect task outcomes (1, 217). Very drastic perturbations can lead to these assumptions being violated. For instance, although missing a target to the left would typically correspond to a leftward motor error (e.g., aiming too far to the left), when acting under mirror-reversed visual feedback this relationship is reversed; a leftward miss actually corresponds to a *rightward* motor error. This incongruence leads to unstable behavior in which errors become exacerbated by adaptive corrections rather than diminished (262), supporting the idea that implicit recalibration relates to updating of an internal inverse model.

How might internal forward and inverse models be encoded? Some hints have been revealed by studies of force-field adaptation in the arm, where the imposed perturbations depend on movement kinematics. Many natural forces we experience depend on the kinematics of the arm: for example, elastic forces depend on displacement, and inertial forces depend on acceleration. We are accustomed to velocity-dependent forces when moving under water, and we even experience lateral velocity-dependent forces through the coriolis effect, when making a reach while our body rotates

(255). Interestingly, in line with how common kinematics-dependent forces are in our environment, adaptation data suggest that the motor system encodes forces in terms of kinematic variables such as position and velocity even when the forces imposed are not explicitly defined in terms of these variables (402, 404, 449). This is consistent with the idea that adaptation arises through updating an internal model of body dynamics, which can be modeled as a function of the positions, velocities, and accelerations of joints, and their cross terms (180).

Variability and the balance between exploration and exploitation in motor adaptation

All movements made, even by neurologically healthy individuals, are inherently variable. Motor variability is commonly regarded as an impediment to successful performance—if a movement were perfect, why should the next one be performed differently? Some recent studies, however, have pointed out that motor variability is not merely noise, but might also reflect the motor system's active exploration for better motor plans for the given environment (81, 479), in line with ideas in operant learning (319, 406). Motor variability in a reaching task increases following unsuccessful movements (335, 437), suggesting that variability can be flexible: if the same movement has repeatedly led to more success than other movements, the motor system can *exploit* this by trying to produce as similar a movement as possible on the next trial, reducing variability; by contrast, if a given movement is unsuccessful, the motor system can increase variability to *explore* for more successful ones in the next attempt.

Importantly for motor adaptation, increased exploration can facilitate the “discovery” of the movement that best counters the perturbation by increasing the likelihood of finding a better action. In line with this idea, Wu and colleagues showed that the speed of adapting to a new perturbation can be predicted by the amount of baseline motor variability (81, 105, 479), and found that training participants on novel types of force fields (different combinations of velocity and position-dependent components) led them to restructure their variability to better align it with the newly experienced environment (479). This shows that exploring the learning parameter space in dimensions relevant to the subsequent perturbation can lead to faster adaptation, as better solutions can be more quickly found (31, 443, 477). The relationship between variability and learning rate is also predicted by a theory in which learning occurs through sequential sampling of actions (150). Accepting and sampling around successful actions, while rejecting unsuccessful actions and backtracking to a previous sample provides a simple but effective method of improving one's actions over time that can account surprisingly well for the time course of learning. Sampling more broadly increases variability but allows for faster identification of more successful actions.

The above studies are more consistent with variability operating via the explicit target-based aiming component of

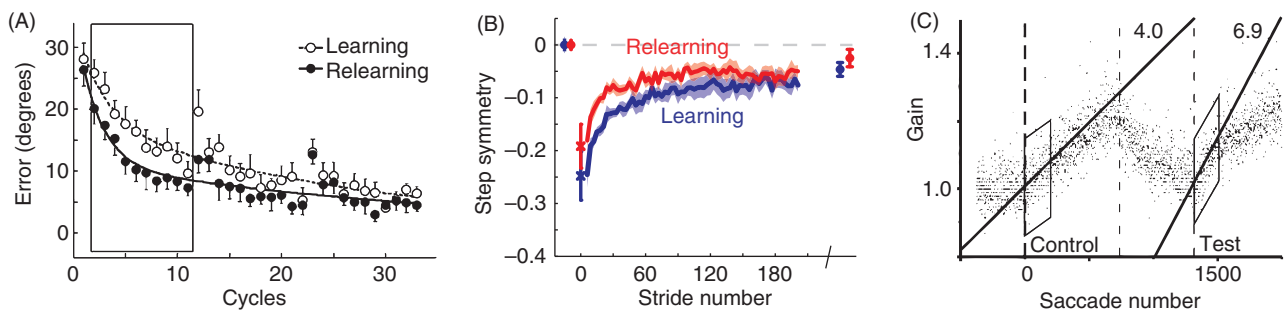


Figure 9 Savings in motor adaptation. (A) Savings in visuomotor rotation adaptation [with permission from (249)], illustrated by the faster reduction in error during readaptation (black circles) compared to initial adaptation (white circles). (B) Savings in locomotor adaptation [with permission from (271)]. In this adaptation paradigm, participants walk on a split-belt treadmill which can impose different speeds on each leg. The introduction of this leg speed discrepancy reduces gait symmetry (y-axis, with 0 indicating perfect symmetry). The restoration of gait symmetry is faster during relearning (red) compared to initial learning (blue). (C) Savings in saccadic adaptation [with permission from (237)]. This study trained monkeys on a positive (> 1) saccadic gain, had them unlearn it by imposing a gain in the opposite direction, and then had them learn a positive saccadic gain again. The rate of relearning was faster, as indicated by the steeper slope in the learning curve. Panels (B) and (C) republished with permission of the Society for Neuroscience from (271) and (237), respectively; permission conveyed through Copyright Clearance Center, Inc.

adaptation rather than the implicit component. Consistent with this interpretation, Fernandez-Ruiz and colleagues noted that, in adapting to visuomotor rotations, participants with more variable reach angles tended to adapt more quickly (105). When participants were forced to move at very short reaction times, however, this relationship disappeared, suggesting that variability was primarily introduced in the explicit component of learning, which has more recently been shown to require greater preparation time to be expressed. (149, 259). Thus, the relationship between variability and learning rate falls firmly outside the scope of state space models of adaptation and even their Bayesian formulation (163, 443, 448). Again, we see how, with more experiments, the adaptation effect of interest, in this case variability, which was initially attributed to the implicit system, gets reassigned to the explicit system.

Long-term memory in motor adaptation

So far, we have focused on adaptation during a single exposure to a perturbation. The phenomenon of decay in adaptation paradigms suggests that adaptation might be just a transient state, lasting little longer than the time it takes to be attained in the first place. That would make adaptation a poor model of motor skill learning in general, which strives to establish robust, long-term skills. Nevertheless, adaptation paradigms do in fact exhibit phenomena associated with longer-term memory and practice, most commonly through savings. Here, under “long-term memory,” we consider phenomena that might manifest any time beyond the initial training session, from minutes to days and even weeks.

Savings

Reacquiring a skill that has already been learned once before (but then apparently forgotten) is typically faster than learning it the first time. Hermann Ebbinghaus, in his magnum opus *Memory: A Contribution to Experimental*

Psychology (96), coined the term “savings” to describe this phenomenon, after observing that he was able to more quickly relearn a series of nonsense syllables that he had learned earlier but had since unlearned or forgotten—thus *saving* him time. Savings is ubiquitous in learning, occurring across different learning domains and paradigms. Examples include cognitive tasks such as recalling words, sounds, or images (267, 316, 317), operant conditioning in animals (114, 291, 315), serial reaction-time tasks (445), and in learning to generate faster, more accurate finger movements (305).

Savings has been extensively studied in motor adaptation, where it manifests as faster learning (fewer trials required) during the second exposure to a perturbation. Savings has been observed in saccade adaptation (237), gait adaptation (271, 283, 361), force-field adaptation (46), and visuomotor adaptation (149, 190, 249, 383, 482). Some examples of savings are shown in Figure 9. Savings is usually examined across exposures that are spaced quite closely in time, usually on the same day or consecutive days. However, savings has been observed even with several days between exposures (249).

It is important to note that if savings is examined before the initial adaptation has been fully extinguished, what might appear as faster readaptation could reflect either faster relearning or residual unwashed-out adaptation from the initial exposure, or a combination of the two. In examining savings, it is crucial to distinguish between these two potential contributions, as the latter does not reflect an improvement in the ability to learn it anew (for further commentary on this distinction, see (247)). Additional caution in examining savings is needed since, when there are multiple components to adaptation, washout might not return all of these components to the original baseline, even if overall performance appears to have returned to baseline. In the case of the two-state (fast/slow) model of Smith and colleagues, the fast washout of the “faster” component masks the incomplete washout of the “slow” one. During readaptation, the partially retained “slow” learning component provides a more advantageous starting

point, resulting in a learning curve that appears faster than initial learning (146, 407). Although this explanation might account for savings in some instances, it does not seem to be the primary mechanism by which savings occurs. For example, savings can be observed even after a prolonged washout period (487), which is likely to ensure that all learning components have returned to baseline; this cannot be accounted for by the two-state model, or any similar state-space model (i.e., linear, time-invariant model with fixed parameters). One way to obtain savings with these models is to allow the learning rate to change across learning sessions (487). This change in “error sensitivity” is in fact exactly what has been recently been claimed to have been demonstrated in a series of experiments (134, 173, 261, 283).

An alternative explanation of savings is that, during washout, the memory for how to counter the perturbation is disengaged and then later retrieved again when the perturbation is reintroduced (190, 334). In this case, there is only an *apparent* rate change but what it is really happening is retrieval over a few trials. In support of this retrieval theory (151), it has been found that introducing an unfamiliar perturbation can prompt participants to retrieve the learned solution to a perturbation that has been experienced before, even if the familiar and unfamiliar perturbations require opposite responses (134, 276, 301). This behavior strongly suggests a tendency to retrieve a previously successful action when encountering *any* error in the future. Indeed, it is possible to generate savings for an unfamiliar perturbation and unfamiliar target, provided the action required to counter the perturbation also happened to be the solution to a previously experienced perturbation (190, 482).

What makes people remember certain actions to retrieve them later? Simply repeating a successful action does not seem to be sufficient in order for it be retrievable for future savings (190, 482). Instead, it seems that what is important is associating the movement with a significantly improved outcome (a positive reward prediction error)—which accounts for the fact that savings seems to be only possible after abruptly introduced perturbations, not gradually introduced ones (173, 261, 482) (since reward-prediction error on any given trial is small in this case), and for the fact that robust savings can occur after as few as five trials of exposure to the initial perturbation (192) (as most of the improvement and, thus, positive reward prediction error, already occurs within this short window). Furthermore, as discussed before, reinforcement also seems to be important for increasing the persistence of adaptation against decay (397).

Given that adaptation is comprised of multiple components, which of these components is responsible for savings? Several studies have shown that savings following a single exposure to a perturbation is attributable to just one component of adaptation. Limiting preparation time to prohibit expression of deliberate components of adaptation eliminates the expression of savings during a second exposure to a perturbation (149). The lack of savings in implicit components of adaptation has also been shown by more directly instructing

participants to withhold any explicit strategy on certain trials (194, 301). Finally, decomposing adaptation into temporally labile and temporally stable components has also shown that slower, more stable components of learning do not show any savings effects (146). These diverse empirical approaches all make a compelling case that savings is an inherently explicit phenomenon mediated by a retrieval mechanism. It is not attributable to a gain change on the implicit component of adaptation. To the extent that error sensitivity does appear to vary with experience, this seems to be related to global behavior in adaptation paradigms, and is broadly consistent with the retrieval theory of savings.

Interference

Learning to successfully compensate for one perturbation can impede our ability to compensate for a second perturbation. This phenomenon, termed *interference* has been thoroughly studied within the setting of force-field and visuomotor rotation tasks (249, 386). For example, let us assume adaptation to a rotation A is followed by adaptation to another rotation B, with A and B typically equal in magnitude but acting in opposite directions. Notably, it is difficult to successfully compensate for both A and B in interleaved trials even with seemingly salient contextual cues (e.g., colors) (5, 120, 142). This interference is termed *anterograde interference*, since learning of A interferes with the ability to learn B in the future. Anterograde interference can be well characterized by state-space models (405) and has been taken to represent an inherent property of the implicit learning system. This conclusion is not entirely unjustified because *if* a contextual cue fails then interference of A on B is consistent with carry-over of aftereffects. However, the apparent purity of anterograde interference in adaptation tasks is complicated by the vexed issue of why some contextual cues succeed in preventing it whereas others do not.

Context can be tricky to define but here we borrow a definition: the contextual signal should be orthogonal to the sensorimotor transformation required for adaptation itself (471). For example, people who wear glasses require the maintenance of two distinct gains of their vestibulo-ocular reflex—one in the context of wearing glasses and one when the glasses are removed. In this case, the contextual cue may be the sensation of the glasses on one’s skin, a sensory modality clearly not relevant for adaptation to lenses. Very interestingly, simple, abstract contextual cues, like the color of a cursor, do not prevent anterograde interference in reaching experiments; participants seem to generalize 100% of their adaptation from one color to another, even if they are fully aware that different colors are associated with different perturbations (5, 120, 142). Nevertheless, certain contextual cues can prevent interference. For example, providing visual cues about the orientation of a virtual object under control (185, 196), requiring participants to manipulate different points on a virtual tool (165), or depicting a different tool altogether (67) can enable participants to maintain distinct adapted states despite these

states having identical movements at baseline. A change of effector prevents interference for visuomotor rotation (247). Adding a lead-in period before an invariant point-to-point movement segment (184) or a follow-through (186,395) also seems to serve as an effective contextual cue to prevent interference when attempting to learn two opposing force fields. This use of pre- or postmovements seems to work even if participants are allowed to pause briefly between the lead-in and the main movement, so long as they occur in quick succession (<0.6 s delay between movements) (184). Interestingly, it even seems sufficient to overcome interference by merely planning a different follow-through, without ever executing it (395). A similar demonstration of the importance of movement *intention* was shown by Hirashima and colleagues (178), who used two opposing visuomotor perturbations to trick participants into using the same movement to guide a cursor toward targets in different locations. Despite the similar movements, participants found it easy to simultaneously adapt to subsequently imposed force perturbations that were different in these two contexts.

So what distinguishes cues that prevent anterograde interference from those that don't? The answer does not seem to pertain to the implicit adaptation process *per se*. Instead the critical factor relates to the movement *goal*; if the cues can be associated with distinct goals then interference can be prevented despite considerable overlap in the details of movement execution for each goal (395). This is profound because it suggests that anterograde interference is not an inevitable low-level motor process but, instead, is a form of high-level cognitive mistake. Colors fail because they do not signify a different movement goal: it is still to make the same straight reach to the same target regardless of whether the target is red or blue.

Another form of interference is *retrograde interference*, which happens when the learning of B interferes with the memory of having previously adapted to A. It therefore manifests as lack of savings for A when A is re-learned after having also learned B. A task design that allows for examining these learning rate differences has the form $A \rightarrow B \rightarrow A$, where the interference of B on the relearning of A can prevent savings in the relearning of A (which would be present had B not been experienced). Using this design, it was found that learning the opposing rotation B reduces savings in the relearning of A (55, 249, 250, 459), implying that learning B interfered retrogradely with the memory formed while learning A.

Initial force-field adaptation experiments suggested that retrograde interference is strongest when training of B immediately follows that of A, and then gradually decreases with time elapsed between those two training episodes, to the point that savings for A is essentially fully restored when the spacing between A and B is about 6 hours or greater (46). This time gradient of interference has been taken as a marker of a gradual consolidation process for motor adaptation, which mirrors analogous findings for the consolidation of declarative memories. However, further experiments were not able to corroborate this graded interference for visuomotor rotation

tasks, with retrograde interference occurring even when the spacing between A and B was 24 h (55,247,249). In retrospect, the unfolding of the retrograde interference story is perhaps less surprising than it might at first seem. As we have already seen in this review, phenomena that were initially associated with the implicit recalibration component of adaptation have since been understood to be properties of the explicit component of adaptation. Savings for visuomotor adaptation is the most notable example (149, 193, 301). We suggested in 2005 that failure to resist retrograde interference was due to two rotations being equally strongly associated with the same reaching goal (247,249). Indeed, when this issue was partially resolved by adding unrotated washout periods before learning either A or B, thereby weakening the association of the same goal with a previous rotation (247), retrograde interference was found after 5 minutes but not after 24 hours, in line with the consolidation gradient shown for force-field adaptation. Thus there may well be a small retrograde interference effect operating on implicit recalibration, but it is swamped by a cognitive phenomenon—a failure to reengage a previously learned explicit aiming strategy because two aiming memories (for A and B) compete with one another for retrieval (247). This theory is consistent with more general theories of declarative memory (470).

Adaptive responses in variable environments

We have earlier mentioned that, when presented with environments in which perturbations can vary from one trial to the next, participants adapt to the expected value of the perturbation. Even when not affecting the extent of adaptation, environmental variability strongly modulates motor responses whose purpose is to maintain stability, such as the grip forces used to maintain contact with the manipulated object (147), the stiffness of the arm used to minimize the destabilizing effect of unexpected perturbations (110, 111, 297, 419), and the magnitude of feedback responses used to restore stability against such unexpected perturbations (112, 134, 486).

The statistics of the distribution of experienced perturbations—or the errors these perturbations caused—can also influence how quickly we adapt. The rate of adaptation has been shown to depend on the consistency of the experienced environment—how likely a perturbation is to persist from one trial to the next; adaptation speed increases in consistent environments and decreases in inconsistent ones (134, 173). Critically, consistency-driven increases in adaptation speed are particularly strong when there is repetition of the exact same perturbation (134).

Apart from adapting to environments, in which the same type of perturbation can vary simply in magnitude, we might also need to repeatedly adapt to sets of perturbations or environments that might vary along a less obvious dimension. For instance, we might have to use different knives that might vary in their size, weight distribution, and sharpness. We would want to be able to rapidly adapt to the specific properties of each knife while not worrying so much about features that

tend to be shared across all knives (a handle at one end and a blade at the other). It has been proposed that people can learn and exploit structure in a learned family of perturbations or environments through a process termed “structural learning” (47, 433, 486). When naïve to the type of a perturbation, the motor system can interpret a given error in many different ways (e.g., a leftward error could be due to a rotation of the cursor, but could also be due to a lateral shift of the cursor, a shear, and so on). The ambiguity as to which parameters are relevant results in slower adaptation. However, after gaining experience in how these perturbation parameters tend to co-vary with one another across different environments, the motor system can restrict its learning within a much more limited space, facilitating learning the next time a similar perturbation is encountered. This kind of structural learning has been demonstrated in adaptation tasks (47, 433, 486). However, it remains unclear whether this learning reflects changes to the properties of implicit learning or to explicit learning.

The neural basis of motor adaptation

Role of cerebellum: prediction

The cerebellum plays a critical role in motor adaptation, as has been established through numerous lines of evidence (73, 390, 410). Cerebellar lesions in monkeys abolish the ability to adapt saccades (25). Numerous studies in patients with cerebellar degeneration have revealed profound deficits in visuomotor adaptation (275, 302, 347, 378, 432), force-field adaptation (68, 129, 277, 347, 408), saccadic adaptation (131, 483), locomotor adaptation (303), and speech adaptation (331). In healthy participants, adaptation appears to be enhanced by anodal cerebellar direct-current stimulation (tDCS) in force-field tasks (172), visuomotor rotation tasks (117), and locomotor adaptation tasks (205) (although the effects of cerebellar stimulation on visuomotor rotation adaptation remain under debate (202)).

It is widely believed that the cerebellum implements a forward model, which predicts the consequences of efferent motor commands during movement [e.g., (472)]. In support of this idea, the cerebellum has indeed been widely implicated in state estimation during movement (293, 483). Furthermore, the Purkinje cells within the cerebellar cortex seem to encode the outcome of an action (such as the trajectory of a movement) (26, 97, 170), rather than the motor commands themselves. It has been suggested that cerebellar nuclei may transform this kinematic prediction into a motor command (170, 171, 290).

It is often assumed that forward models are necessary for predictive control. For instance, when a heavy load supported on one hand is removed by the other, the supporting force is seamlessly decreased at the time of unloading—a behavior that is necessarily anticipatory, due the delays in perceiving the unloading. In an interesting case study, a patient without a cerebellum was found to be unable to achieve such

predictive control (326). With one hand, the patient held a basket into which a ball would be dropped from the other hand. In contrast to controls, the patient was unable to predict the change in grip force required due to adding the ball’s weight to the basket and was thus unable to adjust their grip ahead of impact. Interestingly, however, overlearned anticipatory postural adjustments remain intact in patients with degeneration of the cerebellum in later life (82, 430). These same patients could not, however, learn a new pattern of anticipatory control (82). Together, these results suggest that, although a forward model prediction can be useful for initially learning predictive control, forward model prediction is not always necessary for anticipatory control, particularly for well-practiced movements.

Importantly, cerebellar activity correlates with the presence of errors that can drive adaptation. For example, an imaging study compared cerebellar activation in trials where an error was or was not experienced, and found increased activation during error trials, specifically in lobules V and VI (377). Another imaging study, which modulated the delay between a motor command and the resulting sensory feedback, found that activity in the right lateral cerebellum correlated with the delay, suggesting a representation of the sensory prediction error resulting from the delay (41).

Data from patients with cerebellar degeneration suggest that the cerebellum is specifically involved in learning from sensory prediction errors. Unlike healthy control participants, patients with cerebellar degeneration exhibit very little learning in circumstances where they receive sensory prediction errors in the absence of task errors (423). They also show diminished implicit contributions to adaptation (54). Cerebellar patients are better able to partially adapt to a perturbation that is gradually introduced, compared to one that is abruptly introduced (68, 200). However, when patients do successfully compensate for a gradually introduced perturbation, they fail to exhibit any changes in their perceived movement outcomes, similar to healthy participants who learned to counter the perturbation through reinforcement alone (200). Therefore, spared learning in cerebellar patients likely occurs through a learning mechanism other than implicit recalibration—potentially through trial-and-error reinforcement.

The available neural circuitry in the cerebellum seems well suited to support error-based mechanisms of adaptation. Purkinje cells in the cerebellum receive synapses from two distinct types of fibers: a large number of parallel fibers, which induce simple spike activity in the Purkinje cell, and a single climbing fiber originating in the inferior olive, which induces complex spike activity. A longstanding theory of cerebellar learning, initially proposed by Marr and Albus, is that the strong discharges from the climbing fiber carry sensory error information necessary to update an internal model, which is encoded in the synaptic strength of the much weaker parallel fiber connections (10, 199, 274). Consistent with this idea, adaptation studies in monkeys find increased complex spike activity after introduction of a novel perturbation (409) which persists until successful compensation has been achieved

(130). These activity patterns match the emergence of errors due to the perturbation and their subsequent reduction.

It should be noted, however, that the Marr-Albus theory is not yet proven; in fact, there is some more recent evidence that challenges the role of complex spikes as an error signal. For example, another study found increased complex-spike activity toward the end, rather than the beginning, of the adaptation session, when the error had been reduced (58), whereas another study showed vestibular ocular reflex (VOR) adaptation occurring even when climbing fiber activity is reduced (225); moreover, simple spike activity, not just complex spike activity, has been found to correlate with errors (343).

Finally, as we discussed above, it appears that internal models pertaining to different types of perturbations can be located in different areas in the cerebellum. Rabe and colleagues (347) found that, while patients with cerebellar degeneration showed deficits in adapting to either a force field or a visuomotor rotation, there was no correlation in the degree of impairment across these two tasks. A more recent study used MRI to systematically map specific lesion locations in patients with cerebellar degeneration and investigated how these locations relate to performance in a force-field versus a visuomotor rotation task (86). The finding was that both types of adaptation related to the anterior arm area (lobules IV-VI), with the more anterior part (lobules IV-V) being more involved in force-field adaptation and the more posterior part (lobule VI) in visuomotor adaptation, whereas other regions (crus I and II, which are more commonly implicated in executive control than motor learning *per se*) were involved in both tasks.

Cortex

Galea and colleagues (117) used transcranial direct current stimulation (tDCS) to modulate the excitability of the motor cortex. They found that applying cathodal tDCS to primary motor cortex (M1) led to increases in retention but not in the rate of adaptation. Similarly, anodal tDCS on M1 led to increased aftereffects after force-field adaptation (172, 195). Corroborating these findings, it was found that temporary disruption of M1 using repetitive transcranial magnetic stimulation (rTMS) immediately before adapting to a viscous force-field did not alter the speed of adaptation but did reduce the retention of adaptation the following day (355)—though applying rTMS *after* the initial adaptation to a force-field seems to show no retention deficit (24). In another study, disruption of M1 (but not the premotor area) through single-pulse TMS immediately after the completion of each trial during the learning period in a visuomotor adaptation increased the speed of deadadaptation during a subsequent washout period (144). Together, these results suggested a role for the primary motor cortex in the retention, but not acquisition, of motor adaptation.

Recently, in a novel force-field adaptation task in mice, Mathis and colleagues showed that optogenetic inhibition of the primary somatosensory cortex (S1) extinguished

adaptation but left reward-based learning intact. These findings led the authors to hypothesize that S1 could be involved in storing or updating the internal model mediating adaptation (278), however it remains unclear to what extent the learning in this task is mediated by sensory-prediction-error-based adaptation.

Disruption of the posterior parietal cortex (PPC) using rTMS was found to have no effect on the early phase of adaptation to a viscous force field, but instead resulted in a significant reduction of the level of adaptation reached at steady state (77). In line with this result, a positron emission tomography (PET) study found increased PPC activation during the late phase of visuomotor rotation adaptation rather than initial adaptation (251). Another imaging study of force-field adaptation found increased PPC activation during the post-consolidation recall phase compared to the end of the initial learning period (386), with the shift toward PPC activity also suggesting its role in maintaining a more stable representation of the adaptation. One paper reported results suggesting that adaptation might be lateralized; patients with right parietal damage exhibit normal visuomotor adaptation, while patients with left parietal damage exhibit deficits in adaptation and no aftereffects (312).

Overall, however, we believe it is fair to say that the results above do not comprise a particularly compelling or coherent account of the role of cortical structures in adaptation. Exactly how the cortex contributes to behavior in adaptation tasks remains unclear.

Basal ganglia

A few studies examined patients with basal ganglia disease, generally finding intact adaptation but reduced long-term memory. For example, Huntington's disease patients, in contrast to cerebellar patients, exhibited no deficits in adapting to a force field (408). Gutierrez-Garralda and colleagues (143) found that both Huntington's and Parkinson's disease patients showed normal prism adaptation but reduced aftereffects. In other studies, patients with Parkinson's disease were found to exhibit normal adaptation to a visuomotor rotation but a lack of savings when tested a few days later (30, 260, 272). Moreover, imaging studies have generally found the basal ganglia to be activated during the early phase of visuomotor gain adaptation (251), visuomotor rotation adaptation (384), and force-field adaptation (386), but less so in the late phase. Together, these results suggest that the basal ganglia may play an important role in the more cognitive components of motor learning, but not implicit adaptation, potentially related to the well-established association between the basal ganglia and learning from reward.

Summary: Adaptation

Being able to adapt motor commands to a constantly fluctuating environment is a key aspect of motor control and learning. Indeed, the motor system seems to have developed

dedicated learning mechanisms for maintaining calibration of actions through a cerebellum-dependent, error-driven implicit learning process. This process maintains accurate movement execution. As such, studying adaptation is by itself crucial to understanding how we are able to maintain our existing skill set despite an ever-changing environment. At the same time, it is clear that adaptation tasks probe more than just the brain's capacity for recalibration; implicit recalibration mechanisms are augmented by other learning processes that may influence action selection (e.g., cognitive strategies such as explicit re-aiming) when a participant is attempting to counter an imposed perturbation. The motor system will bring to bear whatever tools it has available on maintaining and improving performance. Adaptation tasks thus rarely provide a pure assay of implicit recalibration and instead are contaminated by the involvement of more general-purpose learning mechanisms. Somewhat ironically, it is the additional learning mechanisms, and not implicit recalibration mechanisms, that are responsible for the lion's share of interesting phenomena in adaptation experiments: savings, interference, and inter-individual variability. Conversely, although adaptation tasks can provide insights into the nature of these general-purpose learning mechanisms, the presence of recalibration mechanisms makes it complicated to use adaptation tasks for that purpose. In any given experiment, it can be very difficult to discern exactly which learning process is responsible for different aspects of learning unless they are deliberately measured as part of the experiment. Consequently, it is

important to remain cautious when generalizing findings from the adaptation domain to the domain of motor skill learning. Ultimately, we suggest that the processes supporting motor skill learning are better-studied using paradigms that more successfully isolate them, as we discuss in later sections.

Sequence Learning

Much effort in motor learning research over the past century has been devoted to studying how a given set of actions becomes organized into a particular temporal order to achieve a task. This set of actions (i.e., the goal) may be a group of discrete movements (such as the set of actions required to prepare a cup of tea), a continuous and overlapping series of events within a single movement (such as the sequential muscle activations required to perform a serve in tennis), or something in between. Regardless of the specific example being studied, however, the manner in which sequences are learned, reproduced, and represented in the brain is believed to be of critical importance to motor control.

Why study sequences?

In activities of daily living, accomplishing any task requires that some sequence of actions be performed to complete an ordered set of subtasks (Fig. 10). These types of sequences require learning the appropriate order of distinct, discrete

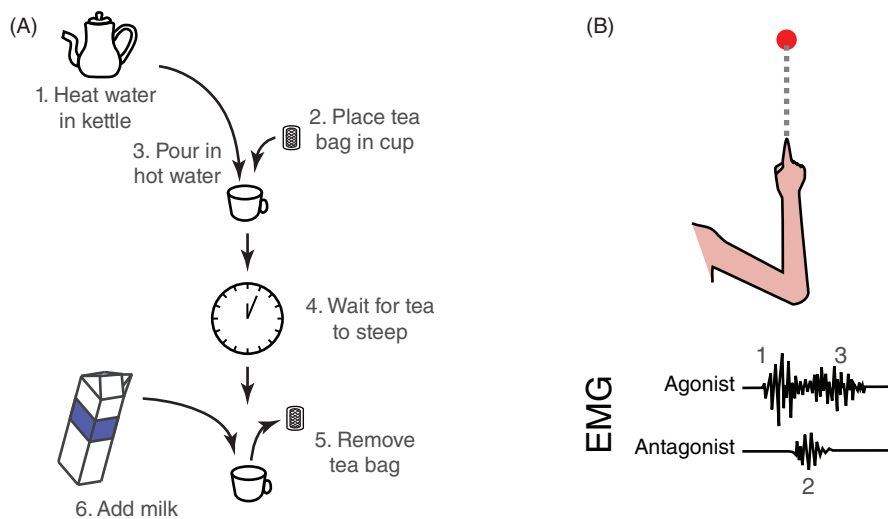


Figure 10 Forms of sequence learning. (A) At the level of the task, sequential order dictates the series of complex, potentially multimovement actions that must be performed to satisfy an overall goal, such as the individual steps required to prepare a cup of tea. Learning to perform these steps in the correct order—largely a cognitive form of learning—has little bearing on the quality of how these steps are executed. (B) At the level of controlling a single movement, muscles must be activated in a particular order to successfully change the position of the limb accurately. Although these steps do not reach the level of conscious thought, the ability for the motor system to execute each sequence element in the correct order and with the correct timing critically affects the quality of the resulting movement. Note that, although these two types of sequences are frequently cited as inspiration for studying the learning of sequences, in practice sequence-learning paradigms largely focus on the acquisition of discrete sequential actions.

actions or steps. For example, making a cup of tea requires steps such as filling a kettle with water, bringing the water to a boil, placing a tea bag in an empty cup, and pouring boiling water in the cup. Although the order of some steps may be switched without dramatic impact on the outcome (e.g., pouring water into the cup before adding the tea bag), other steps have a strict temporal order that is required to be successful (i.e., heating the water in the kettle before pouring it into the cup). This sequence of actions constitutes the goal to be achieved to accomplish the intended task; typically, the individual action elements are already well known, and it is largely the ability to select these actions in the appropriate order that must be learned. Successful execution of such sequences in the correct order may seem trivial, but this ability is disrupted in ideational apraxia, a neurological disorder often observed in patients with Alzheimer's disease (32,342). Another activity of daily living in which sequences play a particularly important role is language. The rules of phonology, morphology, and syntax dictate how sounds and words must be sequenced to convey intended meaning (256), which in turn guide the control of motor speech production. In language, as in other types of sequential behaviors, individual elements become grouped into particular *chunks*—that is, a hierarchical associative grouping structure that aids in the representation and recall of sub-sequences of events during a task (45, 236, 363). For instance, a series of sounds are organized into a word that must be executed by moving the muscles of the throat in a particular order; patients with apraxia of speech produce sounds inaccurately because they have difficulty producing the appropriate sequence of speech movements. In the laboratory, the organization of ordered actions is often studied using simplified tasks such as sequences of button presses or saccadic eye movements. Learning to select each action in the appropriate order (325), and to eventually generate sequences in a largely automatic or routine fashion (366), are of critical importance for many motor skills.

The second distinct notion of sequence learning is that of continuous sequential actions: the idea that continuous, single movements are nevertheless comprised of sequential sub-elements, even if there are no clearly identifiable discrete boundaries between these components. Here the goal of the task can be quite simple, and learning involves changes in the particular action that is selected and how that action is to be executed. For example, the activation patterns of muscles and the movements of individual limb segments during a simple reach (Fig. 10B), and the component sub-movements that form a tennis serve, are two examples of continuous action sequences. The ability to coordinate the order, timing, and duration of muscle activations [e.g., the triphasic burst of activity observed for fast reaching movements (51, 153) or the activity of the six extraocular muscles when generating an oblique saccade (231)] to produce a desired continuous movement requires that the motor system learns to generate the correct time-varying sequence of commands to execute an action accurately (37). Note, however, that this does not

necessarily mean that such sequences need be overtly represented anywhere.

These two ways of conceptualizing motor sequences, i.e., as selection of the correct order of discrete actions versus execution of a continuous sequential action, are quite distinct and should not, in our view, be conflated. The fact that a patient with ideational apraxia can make a normal reaching movement attests to the validity of keeping them separate. Thus, behavioral improvements in these two types of sequential tasks likely require learning at different motor planning stages (Fig. 1). Sequence learning, as it is currently studied, primarily investigates learning the proper order of a sequence of discrete actions (or sub-movements) such that each is selected rapidly and executed accurately (i.e., goal selection and action selection). These tasks are often claimed to be models for the production of continuous movements such as a tennis serve. However, the representations of discrete sequences are almost certainly distinct from those that comprise a single action. For example, discrete sequences are (at least initially) explicitly represented as a set of behavioral rules to be followed (i.e., selection of the correct order of actions), whereas the coordinated sequence of muscle activity that occurs when executing a continuous action never reaches this level of awareness. Furthermore, it seems unlikely that a continuously varying movement is ever represented in terms of a discrete sequence of events. Thus in our view, studies of discrete sequence order have not been and are not likely to be of great use in explaining how a tennis serve is learned or how prehension becomes more accurate. Nevertheless, discrete sequence tasks can teach us a great deal about how the brain learns to abstractly represent orderings of discrete actions.

Sequence learning paradigms

The vast majority of sequence-learning paradigms are concerned with the learning of discrete sequential order. These tasks provide a series of discrete operations that must be performed in a particular order, and then assess how quickly those operations are collectively completed. The sequence elements themselves can be fairly simple and over-learned, such as pressing buttons on a keyboard.

Although seemingly a straightforward question, a number of factors complicate the interpretation of learning the sequential order in such tasks. These difficulties limit the extent to which broad conclusions can be drawn from specific paradigms. In particular, it can be difficult to disentangle learning of the required sequence order from learning to execute the individual movement elements that make up the sequence (128). Another complication is that it can be challenging to disentangle the contributions of explicit instructions and implicit knowledge of the sequence, which have both been hypothesized to contribute to overall sequence performance. Here, we review the current state of understanding of sequence learning and illustrate these difficulties in more detail. First, however, we describe the primary paradigms that have been employed to study sequence learning.

Simple sequences

The simplest sequence-learning task requires participants to practice executing a single, short sequence of about 4-6 elements, typically key presses with different digits of the hand (like playing the piano) (221, 222), with the goal of becoming as fast and accurate as possible at executing the sequence (92, 221, 245, 246, 445, 446, 457). Since the sequence order is explicitly provided to participants at the beginning of the task, the intent of this paradigm is to study improvements in the performance of skilled sequential movements rather than the learning of the sequence order itself. The main finding is that, over days of practice, participants get better at executing the sequence: they move faster and more accurately. Furthermore, participants improve their performance more on the practiced sequence than on other sequences (although there may also be non-sequence-specific improvements, as we shall discuss later).

It is commonly assumed that specificity of learning to the practiced sequence reflects the formation of a new representation of the entire practiced sequence that supports rapid execution. What might the nature of this representation be? It is unlikely to be a change of the individual movement elements themselves, since these components are common to unrehearsed sequences that are not executed so well. Instead, sequence-specific improvements could arise due to getting better at specific transitions between sequence elements. After extensive practice, finger movements tend to overlap temporally with one another, that is, the next finger in the sequence begins to move before the previous one has come to a stop. It is these unique, sequence-specific transitional movements between the individual sequence elements that might become better with practice. For example, practicing the dynamics of switching from the thumb to the index finger might make that particular transition faster than switching from the thumb to the pinky finger.

If it is the case that particular sequence orders do impose unique execution demands, then simple sequence tasks might in fact ultimately probe participants' ability to learn to execute a unique and complex continuous movement—more akin to a tennis serve than making a cup of tea. There is, however, no convincing behavioral evidence for such practice-induced sequence specificity. All studies of simple sequences to date have demonstrated improvements of behavior at the level of the whole sequence (as is consistent with all other sequence tasks), but no study has carefully examined the learning of transitions between individual movements. In fact, a recent fMRI study failed to find any evidence for the representation of a sequence as a single, continuous action rather than the simple summation of its component elements (38, 484). Instead, these findings suggest that sequence specificity might arise for non-motoric reasons, such as improved recall of the order of the individual elements, increases in motivation arising from greater knowledge of the sequence order (474), and the formation of compact, symbolic representations of ordered groups of actions (see Hierarchical organization

section below). Hence, despite the hope that the study of simple sequence tasks that allow overlapping finger movements would provide the insight into motor skill learning in general, at present this paradigm, like the others we will discuss, seems to mainly inform as to how abstract and discrete sequence order is learned and represented.

Serial reaction time task (SRTT)

By far the most prevalent paradigm used to study sequence learning is the Serial Reaction Time Task (SRTT) (322, 358). This task requires movements to be performed in response to stimuli that cue the required response in a spatially congruent manner. Often these movements are finger presses on buttons, although variants of this paradigm have employed other movements such as arm reaches (128, 299), foot stepping (93, 94) or saccadic eye movements (126, 488) toward spatial targets presented in a particular order. Participants are encouraged to respond to each cue as rapidly as possible but not to anticipate it; the next target appears at a brief, fixed delay after the required action has been completed, requiring participants to wait for each target to generate a response. The order in which targets appear (and hence the required order of movement responses) typically obeys a specific, fixed sequence (e.g., a constant sequence of 12 elements), thus allowing participants to learn this order through practice.

Since the SRTT is typically implemented with button presses, the traditional outcome measure has been the total response time—the time from cue onset to the completion of the finger movement to depress the button. Conventionally, the average response time when cues appear in a sequence is compared with the time required to respond to cues that appear in a random fashion (the S-R difference). The S-R difference purportedly provides a sequence-specific measure of learning that is independent of any other sources of improvement, such as learning the mapping between targets and finger presses, fatigue, or other sources of sequence-independent performance improvements. However, the S-R difference may be influenced by cognitive factors such as changes in motivation level, inhibition of the next anticipated movement, or attempts to identify a new sequence order that arise when the targets are suddenly presented randomly.

Unfortunately, there are two major drawbacks of the SRTT as a motor learning paradigm. First, it is, in most cases, not possible to subdivide the gross measure of response time into its component parts—reaction time (RT) and movement time (MT). Practice-related reductions in RT would more convincingly reflect knowledge of sequence order, whereas reductions in MT may instead reflect execution ability of individual sequence elements. Unfortunately, without the ability to dissociate changes to these distinct parameters, it is challenging to identify exactly what kind of motor learning supports overall performance improvements in this task. More recently, attempts have been made to distinguish RT and MT using force-sensitive keyboards to measure finger movements (484), or by utilizing alternative movement effectors such as the arm

or foot (93, 94, 128, 299, 474), which allowed for a clearer dissociation between movement onset and termination. These efforts have suggested that both RT and MT decrease with practice but are not strictly correlated. Nevertheless, the vast majority of SRTT paradigms continue to examine response time. The second difficulty of performing the SRTT with finger presses is that accuracy is assayed as percentage of correct choices (the proportion of trials for which the appropriate action was selected). Hence accuracy in this task is largely concerned with the ability to correctly choose an action given multiple discrete options (or the mapping between stimuli and responses; (438)), but has little to say about the execution quality of those actions (acuity) beyond the small number of studies applying this paradigm to arm reaches as noted above. Thus unfortunately, both of the primary outcomes of the SRTT (and in fact of most sequence-learning tasks)—response time and accuracy—are often misinterpreted.

Nevertheless, the SRTT is thought to demonstrate implicit learning of sequence order. This is because the sequence order is not explicitly provided to participants and simple questionnaires seem to suggest that participants do not become aware of the whole sequence despite exhibiting performance improvements (65, 66, 322, 372, 465). It turns out, however, that participants do in fact explicitly learn sequence fragments, and learning of these fragments appears to fully account for any learning that occurs during this task (299), including the S-R difference. It therefore seems that, as with adaptation, participants do not approach the SRTT in a purely implicit manner; task performance in the SRTT is instead driven by explicit learning of sequence order.

Probabilistic sequence learning

In an attempt to overcome the pitfall of the SRTT not being able to distinguish between implicit and explicit sources of performance improvements, the SRTT has been adapted to feature probabilistic sequences rather than deterministic sequences (189, 208, 209, 381, 411). Specifically, rather than learning a fixed cue order, participants instead learn statistical regularities about the cues, such as the high likelihood (but not total certainty) that a particular cue will succeed another (i.e., the transition probability). By comparing the performance on high-probability transitions to low-probability ones, it is possible to obtain a within-sequence measure of implicit learning. This task can be made more challenging by interleaving elements of a probabilistic sequence with random elements such that participants are required to learn second-order (sequence triplets) rather than first-order (pairs) transitions (188). That is, when predicting the next response, participants need to keep track of the previous two responses instead of only the most recent response. These manipulations are thought to greatly decrease the likelihood that participants can acquire explicit knowledge of the sequence order (208, 209, 381, 411), providing a more robust measure of implicit sequence learning.

This paradigm largely relies upon implicit statistical learning; that is, the ability to detect regularities in the environment that can subsequently be acted upon even if those regularities are not consciously recognized. More formally, statistical learning is a means to discover the relationship between observed inputs and response outputs, for the purposes of predicting future outputs given a particular input (203). Note, this implies that what is learned in these paradigms are the likelihoods of pairs of cues or actions (transition probabilities), not a single representation of the entire sequence as a whole. Moreover, statistical learning may largely occur at a perceptual level (229); participants may learn the likelihood of seeing a particular order of cues appear, rather than directly learning the order of responses, which can be assessed by examining how participants respond when cue-action mappings are changed. Hence, although probabilistic sequence learning provides a more sensitive assay of non-explicit learning about the sequence order, it is unclear whether this learning occurs strictly in the “motor” domain. Nevertheless, probabilistic sequence learning offers intriguing insight into how the brain might exploit statistical learning processes to better generate sequences of actions.

Discrete sequence production (DSP) task

Although used less widely, the Discrete Sequence Production (DSP) task (440) was designed specifically to examine chunking of series of actions into a cohesive whole. In many ways, this task is quite similar to the learning of simple sequences, with the additional challenge of requiring participants to practice two or more short sequences of actions during the same session (e.g., each about 6 keypresses long) to examine the ability to rapidly select the desired sequential response. Indeed, once participants learn the order of actions required by each sequence (i.e., the sequences have become “chunked”), this task becomes one of choosing the correct action sequence from among multiple potential sequences, each cued only by the first element of the sequence. Moreover, responses are encouraged to be largely anticipatory; thus, individuals do not have to wait for each cue to appear before generating the desired response, as with the SRTT, but instead produce a rapid series of movements following the initial cued movement. This avoids the potential confound that participants are learning a perceptual sequence, but cannot distinguish between whether the sequence is a result of learning the order of elements or the formation of a single continuous action.

It is most likely that changes in performance in this task arise from knowledge of explicit sequence order. That is, even more so than the SRTT, performance in the DSP task is likely driven primarily by explicit learning processes. Participants are often informed that they will practice fixed sequences of keystrokes; thus, participants have explicit knowledge of regularity in the order of responses required (83). Moreover, in the DSP, unlike other sequence-learning tasks, performance

is often evaluated after a large number of sequence repetitions (up to 1000 trials (3)).

Hence, although participants often report not having explicit knowledge of the sequence orders by the end of the task (441), this may arise because such sequences become automatized over time due to the large amount of practice (152) and thus become represented in a different manner (22). Although it is often suggested that this new representation is a single motor action consisting of the individual elements (3), we suggest that learning in this DSP task is more likely the result of automatization of knowledge of the sequence order, not of performance of the motor actions, as this paradigm was intended to study.

Other sequence tasks

Aside from the four major categories described above, many other variations on sequence-learning tasks have been used to examine how the brain learns to perform a series of actions. These paradigms include recalling the proper order in which to grasp, pull, and turn handles or knobs on a device (455), learning to estimate a time interval by filling that duration with an idiosyncratic sequence of actions (224), or even performing activities of daily living that are subdivided into sequences of steps (e.g., making a cup of tea). The study of linguistics has also offered many interesting insights and frameworks for understanding the sequential production of sounds and words for speech production. This diversity of paradigms has provided interesting insights regarding how sequences are acquired and retained. Here we highlight a few of these paradigms.

Among the simplest tasks are those that examine the interaction between two actions (168). These tasks, such as the double-saccade task (29, 239, 453), investigate how performance of one action influences the way in which another action is completed. Hence, these tasks at heart are concerned with the learning of a linked pair of actions where the completion of the first affects the transition to the second. In particular, the study of two-element movement sequences have revealed that the second movement of the sequence may be rapidly updated to account for any anticipated or observed spatial errors arising during the first movement (488). This implies that rather than all the elements of a movement sequence chunk being prepared together and then simply played out, the motor plans for subsequent movements may be rapidly updated online as the sequence unfolds (see more discussion on this in the section below “Organizing individual actions into sequences”). To some extent, these paradigms come the closest to the study of continuous sequential actions as they examine the interactions between the individual elements. As with other sequence-learning paradigms, however, there is little evidence thus far that these elements ever become merged into a single movement.

Another interesting variant of the sequence-learning paradigm is the $m \times n$ task, devised by Okihide Hikosaka and colleagues to compare differences in neural activity while

performing well-learned versus unfamiliar sequences of actions (176, 177). In this task, sequences are organized into “hypersets” that require n sets of m buttons to be pressed in a particular order. For example, in a 2×5 paradigm, monkeys are offered a choice of two buttons that must be pressed in a particular order; once correct, a new set of two buttons is offered and this is repeated until the monkey has completed five pairs of button presses. In a sense, a hyperset is a long series of explicitly demarcated chunks; hence, this paradigm can be considered a variant of the DSP task in its focus on learning sub-chunks of discrete actions. By teaching hypersets in this manner, monkeys can become extremely adept at learning a large combination of actions, some of which may even have overlapping chunks, making this paradigm an intriguing one for studying the storage and retrieval of small groupings of actions within longer sequences.

Finally, maze-solving paradigms provide a framework for studying the learning of the sequential order of movement elements such as discrete left/right/up/down actions in service of attaining a broader task goal, that is, reaching a rewarding location within the maze. This task is particularly powerful for investigating how animals, in accordance with a set of imposed task rules, are able to plan novel sequences of actions to attain a goal, rather than simply executing overlearned sequences in a rote manner. This is particularly true when there are multiple solutions to solving the maze. Under such conditions, monkeys are observed to preferentially select the shortest path to reach the target (309, 310). Hence, unlike other sequence tasks that require performance of over-learned sequences of actions, maze-solving tasks allow for the study of how *de novo* sequences of discrete actions are prepared. These maze-solving tasks are quite explicitly cognitive in nature, and may shed light on how individuals choose the order of discrete events to be executed. Such tasks, however, are only “motor” in the sense that movements are used to read out these planned orderings of events, and hence these tasks are quite far removed from the study of motor learning.

The role of practice in learning sequences

As with all investigations into the study of motor learning, the primary focus of sequence-learning paradigms is to measure performance improvements with practice. In most tasks, performance is assessed based on the overall time to complete the sequence (or the average response time in an SRTT paradigm) as well as the accuracy in selecting the correct actions. Response time typically decreases in a roughly exponential manner across a sequence-learning task (Fig. 11). These response-time improvements are thought to arise from a fundamental change in the neural representation of the action sequence, although this may occur primarily at the level of the perceptual-motor mapping. For example, one study examined how sequences were learned by dissociating spatial cues from motoric (key-press) sequences by varying the cue-press mapping, and training participants to learn either a spatial (fixed order of cues) or a motoric (fixed order of finger presses)

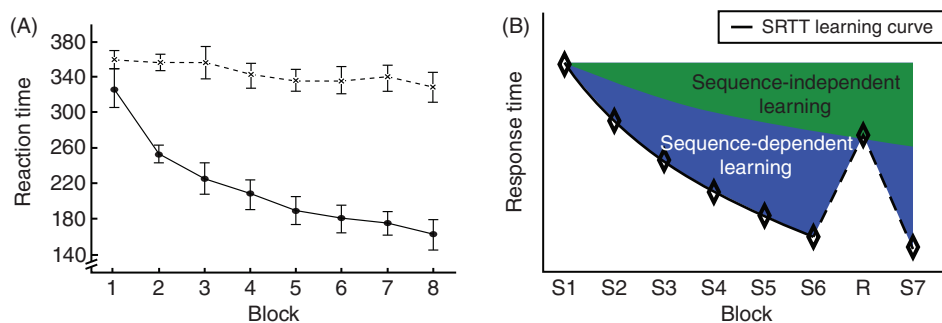


Figure 11 Sequence-specific and sequence-independent learning. (A) When learning a fixed sequence of keypresses (filled circles), response times typically decrease with practice. In contrast, rehearsal of random sequences (x's) also exhibits some improvements in response time, although these improvements are typically smaller. Figure panels reprinted from (322), with permission from Elsevier. (B) Findings such as in (A) suggest that learning during sequence tasks can occur in two ways: improvement of execution of the individual elements regardless of order (sequence-independent learning), and better performance of the elements in a specific order (sequence-dependent learning; this includes knowledge of the sequence). In SRTT tasks, insertion of a random-sequence block (R) toward the end of learning is thought to be a way to distinguish these two forms of learning, although in practice this assay is likely contaminated by additional cognitive influences such as changes in motivation and confidence associated with the unexpected introduction of the random sequence.

sequence; the authors found that neither training scheme transferred well to an SRTT task, suggesting that sequences were not learned in a purely perceptual or motoric manner, but were instead learned at the level of the stimulus-response mapping (465).

Improvements in performance can also occur in between practice sessions (off-line gains). That is, with a sufficiently long break, not only is learning retained, but participants may actually show practice-independent improvements upon retesting (176, 245, 292, 345). This off-line phenomenon is consistent with findings from other learning paradigms (354, 426, 481) and is suggestive of the consolidation of motor memory, although it is only partially influenced by sleep (106, 318, 356, 412). Recent work, however, has called into question the ability to modify learned motor sequences through recall and additional practice (i.e., reconsolidation) by showing that, contrary to predictions of the reconsolidation theory, an existing memory of a learned sequence is not disrupted when individuals retrieve the learned sequence but then practice a novel sequence instead (159). This suggests that some other mechanism may be responsible for the role of offline gains other than reconsolidation. Nevertheless, the gradual improvement in performance with consistent practice of the same sequence, as well as the presence of off-line gains, suggest some form of long-term memory supporting learning. As this is likely to be a process that is not specific to the acquisition of sequences, the study of the role of practice in sequence learning could reveal general principles of learning that can be applied more broadly to other forms of motor and non-motor learning.

Organizing individual actions into sequences

Performing a motor sequence at short latency was initially thought to occur through learning a chained series of the

actions (i.e., a discrete sequential order) (Fig. 12), in that the consequence of each sequence element automatically triggered the next element in a cascade of operantly conditioned behaviors. Since operant conditioning depends upon the repeated reinforcement of each stimulus-response pair in the sequence, it is easy to imagine the response-time advantage that sequentially linking stimulus-response pairs would have over directly cuing each action individually. However, a number of observations are inconsistent with this chaining hypothesis. For one, sequences can be learned and executed without feedback following each subsequent response (this is a critical distinction between the SRTT and DSP tasks, in that for the latter, participants are encouraged to rapidly execute the entire sequence without waiting for feedback about the correctness of the current action). Moreover, at sufficiently low response times, each action would need to be cued by the act of performing the previous action rather than by observing its consequences (although it has in fact been proposed that associations are learned between successive stimulus pairs or successive response pairs (4)). Note that the original chaining hypothesis could be modified to require only knowledge of which action was previously executed (in a feed-forward sense) rather than observing the consequences of that action. However, this does not avoid the final inconsistency associated with this hypothesis, namely that one should be able to start anywhere in the sequence and automatically trigger the remainder of the sequence to be executed in order without pause; instead, it has been shown that starting in the middle of an action sequence is quite challenging (337).

Alternatively, it has been proposed that learning sequences of actions relies upon the merging of individual elements into a more encompassing, higher-level representation of the sequence itself (Fig. 12). Specifically, as sequences are learned, an abstract representation of the sequence order is formed (for more discussion, see the section on “Implicit and

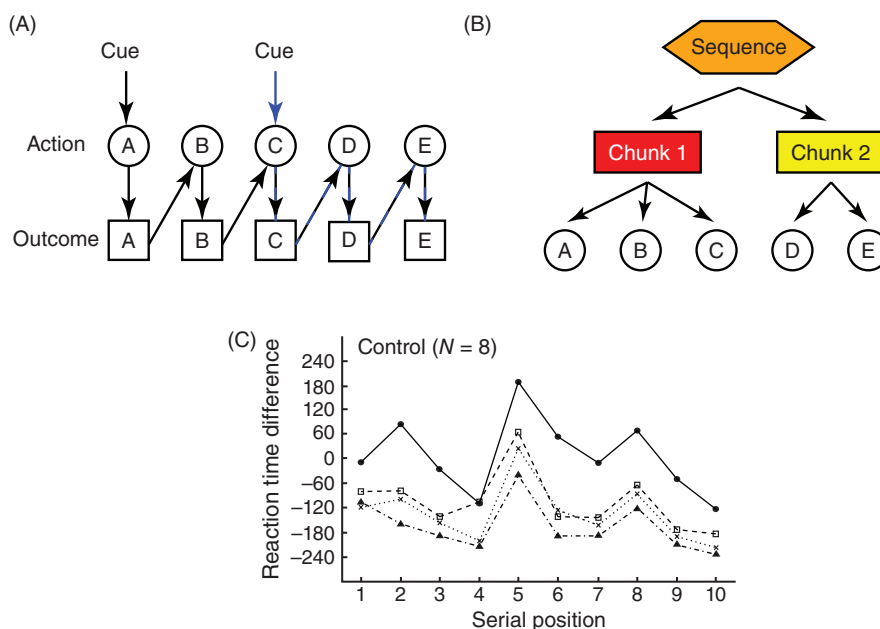


Figure 12 Representations of learned action sequences. (A) According to the traditional version of the simple chaining model, each element of a sequence is cued directly by the observable outcome of the prior sequence element. Thus, cueing element A automatically leads to a series of events that produces the remaining elements in the appropriate order (black arrows). This model would predict that cueing an element in the middle of a sequence, such as element C, would result in the execution of a partial sequence of all the remaining elements (blue dashed lines). More recently, it has been suggested that these chains do not necessarily link observed outcomes to action, but could be links that exist in the purely motor or stimulus domain. (B) The hierarchical model proposes that individual elements are organized into increasingly larger chunks that ultimately are assembled into a single sequence representation. While individual chunks can be cued, cueing element C in this case would not lead to a partial sequence since performance of element C does not automatically trigger Chunk 2. (C) Previous research has suggested that sequence chunks can be identified using variations in RT within a sequence. RTs between some pairs of elements tend to be consistently longer than between other pairs, suggesting a hierarchical organization in which elements within a single sequence chunk are triggered together, with additional preparation required between chunks. For example, in this figure, average response times (normalized to baseline performance) are illustrated for each of four practice blocks across a single sequence-learning session (block 1, filled circles; block 2, open squares; block 3, x's; block 4, filled triangles). Serial positions 5 and 8 have consistently prolonged RTs compared to that of the other elements, and are suggestive of being the beginnings of two successive sequence chunks. Figure panel reprinted from (322), with permission from Elsevier.

explicit forms of sequence learning” later). That is, rather than representing each individual sequence element, a higher-level representation of the entire sequence may emerge to allow for a compact means of representing, planning, and recalling the entire sequence of actions (see section below on Chunking). In that way, the entire sequence of actions may be planned in advance prior to the initiation of the first action, and then executed in the order in which the individual elements were planned. Indeed, the discrete sequence production (DSP) task reveals that, once learned, an entire sequence of actions can be cued by presenting only the first target stimulus of the sequence. Two critical observations support this hierarchical-learning hypothesis. First, the RT of the first movement tends to increase with the length and number of unique elements in the sequence (160, 168), at least for sequences of up to about three to five elements. Second, execution of the initial movement is modulated by subsequent movements, suggesting

that several movement elements may be planned together; in two-element simple sequences, for example, the accuracy with which the initial target is performed is modulated by the accuracy level demanded in the subsequent movement (400).

This higher-level abstraction of the entire sequence does not imply that once the sequence elements are planned, there is no way to modify those individual plans as the sequence is being executed. For example, actions that are performed later in the sequence can be updated to account for errors generated on earlier elements of the sequence. This effect is especially clear in the double-saccade task, in which the second movement of the sequence can be rapidly updated to account for spatial errors arising during the first movement, even when those errors cannot be directly observed (e.g., if the first saccade is executed to the remembered location of the first target rather than to a visible target location) (29). This finding implies that even if all the elements of a movement sequence

are prepared together before the first sequence element is executed, the motor plans of the subsequent movements may be revised as the sequence unfolds rather than simply playing out as they were initially planned (488). Alternatively, whereas the order of sequence elements is determined in advance, exactly how the individual elements are executed may not be fully planned before the first element in the sequence is executed—that is, discrete sequences may not be planned as a single executed movement in the same way that continuous actions likely are.

Sequence-specific and sequence-independent learning

There are clear benefits associated with performing actions in specific sequences. Practice during sequence tasks can have a sequence-specific performance benefit (Fig. 10B): a well-rehearsed sequence can be performed at low response times compared to novel or random sequences. However, a second, sequence-independent effect can also be observed: practice of the individual sequence elements, regardless of sequence order, is sufficient to confer a performance advantage when the elements are combined in a sequence. Individuals who practice in the random condition, which is often used as a control when examining sequence learning behavior, also exhibit some decreases in response time (322, 474) (Fig. 11). In fact, in the SRTT paradigm, researchers seek to account for this sequence-independent learning effect by comparing post-training response times for key presses between sequence and random-order blocks (i.e., the S-R difference) on a per-subject basis; the difference between sequence and random blocks at the end of training is thought to reflect sequence-dependent learning alone by removing sequence-independent learning (although this difference may be contaminated by additional cognitive effects, see the section on “Serial Reaction Time Task” earlier). Moreover, monkeys performing the 2×5 task not only exhibited faster response times for well-rehearsed sequences, but also required fewer trials to learn novel sequences as training progresses, suggesting a meta-learning of the overall paradigm structure and how to more quickly perform each individual selected action (176). Finally, typists who were asked to practice typing a set of words that contained a specific set of letters displayed a performance advantage when they typed new words that included those rehearsed letters compared to words formed from untrained letters (72). This performance transfer to novel words in a sequence-independent manner suggests that sequence-independent practice effects associated with individual movement elements are quite robust, and need to be distinguished from sequence-specific performance advantages. Ironically, this sequence-independent learning arising from practice—the aspect of sequence-learning paradigms that is considered a contaminant and is not well studied—may be the portion of these tasks that actually reflects motor learning.

Hierarchical organization of sequences

One of the critical features of sequence learning is the idea that once learned, individual sequence elements are no longer represented and executed independently but are instead grouped together (379) through a neural representation that encompasses the activity associated with the collective set of sequence elements. This representation can then be simply played back on demand (168). This notion was supported by evidence that the RT for the first movement increases as the number of subcomponents of the required action increase (168, 417), suggesting that the entire ordered set of actions may be recalled from memory before the first element is initiated. Thus instead of having to plan each individual movement independently, the entire sequence of actions may be executed as a single movement pattern because each future discrete action and each transition between pairs of discrete actions can be anticipated, and this ordering information is retained in a buffer to facilitate rapid execution (20, 439).

Many sequences of actions, however, can be quite long and complex, and there appears to be a finite capacity to the ability to group multiple, individual movements into a single set. Long sequences are often divided into short response segments of about 3–7 elements (50, 295, 322, 370). These sequence “chunks” are demarcated behaviorally by an increase in response time compared to the response times of subsequent elements within the chunk (370) (Fig. 12C); this longer response time for the initial chunk element is thought to represent pre-planning or recall of the entire chunk to be executed (370, 439). However, more recently it has been suggested that these changes in response time might instead reflect idiosyncratic behaviors or biomechanical constraints rather than marking the organization of chunk structures (207). Nevertheless, to the extent that sequences are organized into chunks, this organization is largely a means of cognitively grouping elements into pieces to make the learning of a sequential order more tractable; there is currently little evidence that individual actions become “chunked” together at the motor level to form continuous actions.

The length of each chunk and the chunking structure of a sequence may ultimately be determined by working memory capacity (42), and may in part be associated with the extent to which information (in a mathematical sense) in a sequence is best compressed (279). Regardless of how chunks are determined, however, the use of chunks provides a way to recall very long sequences in which the number of individual elements (but not the number of chunks) exceeds working memory capacity (295). Similar use of a chunking representation facilitates expert recall of long lists of words or numbers, dense street maps, or arrangements of chess pieces on a chessboard (100).

Formation of sequence chunks

Chunking tends to occur by first learning simple transitions between pairs of responses (93, 263, 336) (i.e., the smallest

fragment of sequence order possible) as a form of associative learning (4), although this remains to some degree stimulus-dependent. This associative learning typically happens simply through repetition of co-occurrence of the same groupings of particular actions, and may be thought of as a form of statistical learning (339). As practice proceeds, however, it is thought that longer sequence fragments are learned (52), which may form the basis of sequence chunks. These sequence chunks can then be executed relatively autonomously. That is, after cuing the first response, the remaining actions are thought to rapidly play out without requiring additional cues.

Since chunking tends to occur spontaneously, this organizational structure presumably confers a performance advantage. Indeed, it has been observed that new sequences formed from the rearrangement of previously practiced individual chunks in a different order, are performed more quickly compared to random sequences (370), although they are not performed as rapidly as the original sequence. This suggests that participants not only learn the order of elements within a chunk, but also learn about the order or transitions between chunks (349). Chunking can even develop spontaneously offline as the sequence is being consolidated (478). However, when a less motorically optimal chunking structure is taught initially, such as when a sequence is intentionally divided such that breaks between chunks occur in the middle of runs and trills (i.e., an alternation between two sequence elements), that inefficient structure remains preserved despite long periods of practice of the entire sequence without an enforced chunk structure (344). This observation again suggests that chunking is largely a means of organizing an order of elements rather than optimizing their execution. Finally, learned chunk structures are task-dependent. For example, rehearsing two short, four-element sequences that occur with different prevalence but share a single common pair of responses does not necessarily mean that the consistently repeated pair of actions will be chunked; instead, a response time advantage is only observed during the well-rehearsed complete sequence (336), perhaps because participants treated the entire four-element sequence as a single chunk.

Importantly, as already alluded to above, the issue has been raised of whether higher-order representations (i.e., chunks) of sequences are actually represented motorically or if they only exist at a more abstract level. Lashley proposed that higher-order representations reflect the order of elements in an abstract sequence rather than the motoric details of the individual elements themselves (256), consistent with the argument that sequence learning is primarily concerned with acquiring knowledge of the sequence order rather than grouping simpler movements into continuous complex actions. In support of this view, recent evidence has suggested that sequences of finger actions can be learned symbolically via color cues and then immediately applied to saccadic eye movement sequences (415), arguing for an abstract, effector-independent chunking representation. Additionally, it has been suggested that simply observing a sequence confers a performance benefit equivalent to actual

motor practice [(187); but see (462)], and that sequences that resemble the training sequence either motorically or perceptually are performed better than novel sequences (103). Furthermore, rules about the sequence order can be transferred to new sequences (i.e., analogical transfer) by changing the absolute movement elements but preserving their relative relationships in the sequence (i.e., a rule may be that the previous two elements in a sequence chunk repeat at the start of the next chunk, but the exact identity of those elements may differ from one sequence to another), suggesting a hierarchical representation that is action independent but order dependent (84). Finally, when participants are not given advance knowledge about the number of elements in the sequence, the modulation of RT consistent with development of a chunking structure is not observed (227), again suggesting that chunking is largely a cognitive strategy to organize individual sequence elements into simpler, order-based representations. Hence, to the extent that sequence learning can inform us about chunking and hierarchical organization of action sequences, the majority of the evidence suggests these grouping structures are likely to be cognitive rather than execution related.

Indeed, some of the strongest evidence that chunking occurs at the level of learning order and not at the level of action execution comes from recent neuroimaging studies. If sequence learning involves a grouping of discrete actions into a single, continuous movement, one should expect to observe the formation of a new representation for this novel continuous sequential action in motor cortex. However, recent work has revealed that neural activity in M1 does not contain any sequence representation but can instead be explained by the activity required to produce the individual elements of the sequence (484). Moreover, even after five weeks of training, the representations of the individual fingers remain consistent at every level of the motor hierarchy, despite learning to generate certain pairs of finger transitions at higher frequency than other pairs (38). These findings again suggest that sequence-learning tasks primarily probe the formation of a cognitive organizational structure describing sequence order, which then operates on unchanged single motor elements for execution. Thus, chunking remains distinct from generating a single continuous movement such as a tennis serve, in the sense that the knowledge of the order rather than the actual constituent movements become represented as a single entity. Evidence of novel motor-execution-related representations of specific, full sequences remains elusive.

Once sequence chunks have been formed, this grouping process is thought to be repeated upon the chunks to form a single, abstract representation of the entire sequence (19,236,363). However, as this organizational process is presumed to be similar at each level of the hierarchy, research efforts have remained focused on the initial chunking stage, or have been restricted to the study of reasonably short sequences of actions. Moreover, identifying these more abstract representations and finding behavioral markers of their existence remains challenging. The best evidence about the abstract

nature of this hierarchical organization at the level of chunks and beyond comes from studies of generalization.

Evidence of hierarchical organization: Generalization

Generalization examines the ability to transfer learned performance improvements to other effectors (e.g., the other hand) or to novel but similar sequences. The finding that sequences can generalize provides evidence that representations of entire sequences are not movement-specific (66, 226, 330). This is not surprising given the evidence reviewed in the previous section indicating that the constituent chunks comprising a sequence are already likely to be representations of order rather than continuous motor actions. Even if that were not the case, however, generalization would provide compelling evidence that, at the highest levels of the organizational hierarchy, sequences are learned as cognitive representations of order. For example, individuals who are trained to perform a sequence with one hand can perform the same sequence much faster than a novel sequence using the opposite hand (115, 137). This generalization benefit occurs when the untrained hand performs the sequence in extrinsic coordinates (e.g., the same buttons on a keyboard), but also can be observed to a lesser extent in intrinsic coordinates (e.g., the same finger on the opposite hand) (137). This is consistent with the finding that sequence representations in both extrinsic and intrinsic coordinates can be observed in different regions of the brain (458). Generalization of the chunking structure can be observed when individuals that were trained to generate a sequence using three fingers on one hand were subsequently asked to perform the same sequence using a combination of fingers across both hands, or vice versa (442). Finally, if participants switched their hand positions on a keyboard so that different fingers were required to press each key, performance of a sequence was maintained when the sequence of key-presses was preserved but not when the actual sequence of finger movements was preserved, providing strong evidence that the sequence was represented in an effector-independent manner (467). In contrast, any sequence-specific learning that remains movement-specific and does not generalize could reflect learning about the mechanical interactions (e.g., dynamics of the transitions) between the movements required by each of the individual sequence elements.

At a more complex level, experimenters have examined intermanual generalization after learning bimanual sequences. For example, Berner and Hoffmann examined learning of a bimanual-bisequential SRTT task, in which each hand performs a unique sequence simultaneously (34). They demonstrated that although the two hands always practiced the sequence simultaneously, each hand learned the sequence independently to some extent; performance when one hand performed the learned sequence and the other performed a random sequence was still better than when both hands performed random sequences. Moreover, some amount of intermanual generalization also occurred when each hand simultaneously

performed the sequence learned by the other, arguing that the two sequences were learned at least partially in an effector-independent manner (34). However, more recent evidence has shown little generalization from learning to perform two simultaneous sequences bimanually to executing only one of those sequences unimanually, suggesting that such tasks may not simply be represented as a pair of unimanual sequences but instead as an integrated whole involving coordination of the two hands (485). Similarly, simultaneously learning a visual and auditory sequence appears to generate an integrated representation in which performance degrades if either the visual or the auditory sequence is disrupted (174, 380). While these findings are suggestive of some effector or modality-dependent components in sequence learning, the large amount of successful generalization that has been observed across multiple motor effectors and sensory modalities implicates the largely cognitive nature of sequence representations.

Implicit and explicit forms of sequence learning

As we have discussed, a common assumption about sequence-learning paradigms is that learning takes place in the motor domain; that is, that sequence learning is in large part about creating a single, implicit motor representation that encompasses the entire set (or chunk) of actions to be executed. Thus, sequences are assumed to be executed as if they were a continuous, sequential action, supporting the argument for a parallel between the generation of motor sequences and the control of muscle activations that occur during a single action. Moreover, this has led to the general assumption that the order of the individual elements is implicitly represented, and not necessarily explicitly known. The logic, therefore is that, if motor skill learning is largely implicit (or at least has a significant implicit component; see the discussion in the introduction to this review), and if motor-sequence-learning paradigms are a reasonable model of motor skill learning, then sequence learning must be implicit (or at least have a significant implicit component). To that end, much effort has been invested in trying to verify this assumption, seeking evidence that sequence learning is not simply cognitive learning of order combined with non-specific practice effects on individual elements (299, 474). In our view, this endeavor has been unsuccessful.

The idea that sequence learning is implicit arises from two major lines of evidence. The first line includes studies demonstrating lack of awareness of the presence of a sequence. For example, use of pharmaceutical interventions that suppress sequence awareness in healthy individuals had little measurable impact on their ability to learn the sequence (323). In addition, studies involving patients with amnesia are thought to be strong evidence of implicit sequence learning because these patients have severe impairments in declarative knowledge, and presumably can only acquire sequences by relying on implicit learning (74, 322, 324, 351, 352) (Fig. 13A). In one study, for example, the authors found that although patients with Korsakoff's syndrome generally

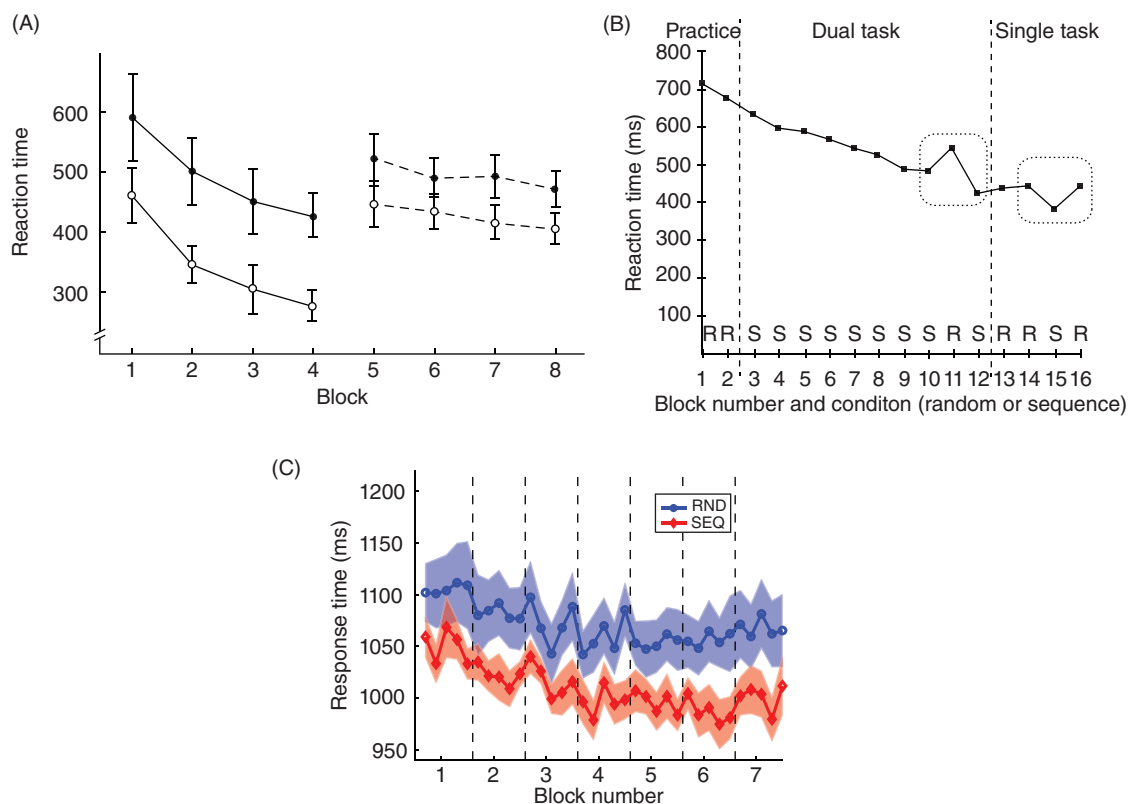


Figure 13 Evidence for implicit and explicit sequence learning. (A) Response times of Korsakoff patients (filled circles, who have declarative-memory impairments) and healthy age-matched controls (open circles) reveal that although patients are in general slower, they can still learn to improve their response times during practice of a fixed sequence (blocks 1-4). This improvement in response time is greater than that observed during rehearsal of random sequences (dashed lines, blocks 5-8). Neuropsychological findings such as this provided one piece of evidence supporting the assertion that sequence learning is implicit, as it does not require declarative memory. However, patients do not perform as well as controls in general, and there is no definitive evidence that patients do not rely on declarative memory for trial-to-trial learning. Indeed, patients with amnesia do retain the ability to report knowledge of sequence fragments (351, 352). Panel reprinted from (322), with permission from Elsevier. (B) Despite the presence of a secondary task, participants are able to improve their performance of a first-order sequence. The extent of learning under dual-task conditions (measured by the S-R difference in block 11) was found to be comparable to the S-R difference when the secondary task was removed (block 15), suggesting that the secondary task had no impact on the extent of sequence learning that took place (i.e., that sequence learning does not require attentional resources). However, the majority of learning that did occur under dual-task conditions appears to be sequence-independent learning, as indicated by performance in the Random blocks. Panel reprinted, with permission, from (75). (C) Wong and colleagues (474) contrasted practice of a fully explicit sequence (red diamonds; taught to participants prior to training) and movements toward randomly appearing targets (blue circles). They observed an immediate improvement in response time reflecting the explicit sequence knowledge, and gradual improvements with practice. Because the learning rate of these gradual improvements did not differ between the sequence and the random groups, these practice-related improvements in response time reflected sequence-independent learning; there was no evidence of any implicit sequence-specific learning. Adapted, with permission, from (474).

exhibited slower response times compared to controls, both patient and control groups exhibited gradual decreases in response time during an SRTT task (322). Since these patients have amnesia, it was assumed that they could not be learning the sequence explicitly; thus, this finding has been cited as evidence that sequence learning is implicit. However, the patients in this study did not learn or perform the task as well as controls; the difference in response times between patients and controls was larger during the sequence blocks compared to random blocks, and keypress accuracy was worse overall for patients regardless of whether there was a sequence or not. A large part of sequence learning and execution may therefore still rely on declarative memory. Additionally, as

noted in the introduction, if an amnesic patient learns a motor task, this does not rule out the possibility that declarative processes contributed to trial-to-trial learning. Hence, these findings do not provide convincing evidence that sequence learning is implicit. Finally, although patients were found to have little ability to recognize or verbally report the sequence order, control participants in many studies have demonstrated a similar inability to report the sequence depending on exactly how explicit knowledge of sequence order was assayed (65, 66, 322, 372, 465). In fact, patients with amnesia can exhibit some fragmentary knowledge of the sequence during verbal reporting (351, 352), and when asked to predict the next element in the sequence they perform comparably

to controls and better than participants that only practiced random sequences (351).

In a separate study, although there was no clear indication of a learning difference on an SRTT task between amnesic patients and controls, these same patients were found to exhibit impaired learning in a maze task, in which they had to learn the sequence of turns to get through a maze (324). After about 10 blocks, completion times plateaued for patients but continued to decrease for controls. Why patients with amnesia should be able to learn the order of simple finger presses but not the order of turns in a maze is something of a puzzle. One suggestion is that although some sequence tasks can be learned according to first-order associations, in which it is possible to anticipate the likelihood of the next action simply from the frequency of action pairs experienced during training, patients are more impaired when it comes to learning second-order associations because this stresses the declarative system to a greater extent (74). Presumably, navigating a maze requires knowledge of the current position in the maze and not simply the identity of the previous turn, which makes this task analogous to the learning of higher-order sequences. Hence, declarative memory may be stressed more when learning complex sequence patterns. Alternatively, statistical learning might support the learning of simpler sequences under conditions when declarative memory is impaired (18,339), although statistical learning will not give rise to a continuous motor action representation in the way that implicit sequence learning is thought to do. Furthermore, admittedly at the risk of reverse inference, one imaging study has suggested that the hippocampus is activated even when participants express no awareness of the sequence to be learned, suggesting that the hippocampus (and thus declarative knowledge) may be important for learning sequences even when explicit knowledge cannot be detected (376).

The second line of evidence regarding the implicit nature of sequence learning comes from studies examining the role of attention in the ability to learn sequences. This line of reasoning makes the assumption that implicit learning should require minimal attentional resources and thus should proceed unhindered despite the presence of a distracting secondary task (66, 113). While it has been found that dual tasks tend to decrease performance in sequence-learning tasks compared to individuals who are only performing the sequence alone (323) (Fig. 13B), the S-R difference (between sequence and random blocks) under dual-task conditions was comparable to the difference assayed under subsequent single-task conditions (75). This evidence has been used to argue that attentional resources were not necessary to learn sequences. However, the majority of improvements in this task actually arose from sequence-independent rehearsal of the individual movement elements based on measured performance in the random condition. Additionally, to the extent that participants learn sequence structure in a dual-task condition, most of that sequence knowledge is acquired within the first block of trials (113), suggesting that much of this sequence-specific learning could be explicit. Finally, participants are really only capable

of learning first-order sequences well under dual-task conditions (66), either because these sequences follow simple rules that can be explicitly acquired or because participants rely on statistical learning. In neither case is it likely that participants ever implicitly acquire a representation of the full sequence. Finally, the performance improvements in dual-task conditions could easily arise from learning of the ability to dual-task, rather than learning about the sequence *per se*.

Efforts to convincingly demonstrate attention-independent learning in dual-task conditions have turned to the use of probabilistic sequence learning tasks combined with attentional distractors. Although participants use explicit knowledge in the form of cues to learn the probability of where the next target will appear, when those cues are removed or when participants are placed under dual-task conditions, some implicit sequence knowledge regarding the likelihood of the next action is thought to remain (63, 209). It has thus been argued that sequence learning in this paradigm is implicit. However, it has recently been demonstrated that even when required to perform a dual-task symbol-counting paradigm involving probabilistic sequence learning, participants acquire explicit knowledge as assayed by the ability to intentionally generate patterns that match or do not match the learned sequence (394). In fact, performance on these explicit assays is indistinguishable between participants learning under dual-task conditions and learning of the sequence alone (394). This suggests that dual tasks, even those that involve probabilistic sequence learning, are not effective at eliminating the acquisition of explicit sequence knowledge.

The debate regarding whether participants acquire explicit sequence knowledge—assayed through awareness, recall, recognition, or the ability to generate or predict the next element in the sequence—and the extent to which that knowledge can account for observed sequence learning, has been at the forefront of the sequence-learning field for quite some time (65, 79, 337, 338, 372, 393, 463-465). It has been illustrated that if one probes carefully, there is always evidence for explicit knowledge of the sequence order in most SRTT tasks. Whether that knowledge is useful and contributes to sequence learning has been debated, but it is undeniably compelling that the time course of learning explicit sequence fragments typically precedes or coincides with the time course of performance improvements (52, 128). In fact, spatial accuracy to visually cued targets improves specifically for those movement elements that were declaratively known in advance and could therefore be anticipated; no performance changes were found to precede the acquisition of declarative knowledge (299). Moreover, attempts to dissociate explicit from implicit learning processes by providing individuals with explicit sequence knowledge in advance have revealed that all performance improvements can be accounted for by the possession of explicit knowledge and non-sequence-specific rehearsal of the individual movement elements (474) (Fig. 13C). Therefore, although many studies of sequence learning claim to focus on implicit motor learning, sequence tasks appear to be learned primarily at a cognitive level by acquiring explicit

knowledge of the sequence order. Any implicit learning that occurs might be accounted for by some form of learning about the transitions between pairs of sequence elements (e.g., statistical learning or potentially by learning the dynamical transitions between elements), automatization of knowledge that was initially learned in an explicit manner, or sequence-independent improvements of the individual movement elements. Even if there were convincing evidence for implicit learning of sequence order, this is unlikely to relate to merging of discrete elements into a single continuous action representation.

Neural representations of sequences

Given the discussion above, we suggest that most neural correlates of sequence learning pertain to representations of sequence order. This is particularly true as most sequence elements involve well-practiced actions like button-presses or saccades, for which further improvement in the execution of the individual sequence elements is unlikely. Thus, any detectable neural changes that occur during sequence-learning paradigms employing such movements, after controlling for sequence-independent learning, are likely to be directly linked to learning the sequence order (although it is important to also control for performance confounds associated with executing the sequence faster or more accurately). Efforts in particular have been directed at searching for neural changes in motor cortices that correspond to the learning of sequences with the hope of observing the formation of representations of continuous action sequences. These investigations, however, have largely failed to identify any such changes. While learning to link groups of preexisting movement elements into novel action sequences has been found to depend on having intact motor cortex in rats (224), the primary motor cortex in primates may be necessary largely to perform the requisite actions in the sequence rather than to learn anything sequence specific (308). Indeed, it has been difficult to find any learning-related changes associated with neural activity in primary motor cortex in humans [see, e.g., (38, 484)]. This supports the view that sequence learning in these paradigms occurs through improved cognitive representations of the sequence order rather than learning an inherently motoric representation. While not the intended focus of efforts to study implicit sequence learning and the formation of continuous sequential action representations, such cognitive representations are nevertheless intriguing as an important aspect of motor skill learning.

On a broader level, attempts have been made to apply neuroimaging to observe changes throughout the brain as healthy individuals learn and execute sequences. Activity changes have been noted in many brain regions spanning prefrontal and premotor areas (136, 137), as well as subcortical areas including the basal ganglia and cerebellum (Fig. 2). However, it is unclear whether learning-related activity in these areas is best attributed to implicit (e.g., statistical) or explicit (e.g., knowledge of order) sequence learning. Although some

studies have argued that distinct regions are engaged in implicit versus explicit sequence learning (136, 162, 181, 350, 371), other studies have argued for a partial or even a complete overlap of regions involved (371, 466). This confusion arises in part because of the difficulty in assaying whether sequence learning can ever occur without an explicit component (see section on Implicit and Explicit, above), or even whether any implicit learning that arises is simply the automatization of an explicitly learned element order. Thus, while sequence-related changes in neural activity can be observed during sequence-learning tasks, it is not possible to draw a distinction between the neural correlates of implicit and explicit sequence learning.

Cerebellar contributions to sequence learning

The role of the cerebellum in sequence learning is less clear than its role in adaptation. For example, activity in the cerebellum has been observed to both increase (89) or decrease (90–92, 109, 136, 206, 218, 434) as learning proceeds. Nevertheless, the cerebellum is thought to have a greater role than simply supporting the execution of individual actions: unlike healthy controls, patients with bilateral cerebellar lesions exhibited no reaction-time advantage in generating each element in a fixed sequence compared to performing each element alone (197). Moreover, muscimol injections to inactivate the dentate nucleus in monkeys led to an increase in errors for well-learned sequences (265). Whether the cerebellum is necessary for actually learning sequences, what it might contribute to this process, and how these hypotheses relate to the current view that the cerebellum computes sensory-prediction errors, all remain unanswered questions.

The basal ganglia modulate sequence-specific performance

Activity in the basal ganglia—particularly in the posterior regions of the putamen—tends to increase as sequences are learned. Using fMRI, it has been found that activity in the putamen (i.e., in the sensorimotor regions of the basal ganglia) is correlated with the performance of well-learned sequences (23, 90, 91, 109, 218, 434). More rostral, association regions of the basal ganglia have been implicated earlier in learning (258). Consistent with these imaging studies, muscimol inactivation of different regions of the basal ganglia in monkeys appears to influence different stages during sequence learning paradigms: inactivation of the anterior caudate reduces the ability to learn a sequence, whereas inactivation of the middle-posterior putamen increases the number of errors made during well-learned sequences (298). As with the cerebellum, however, it remains unclear exactly what the basal ganglia might contribute to these processes.

One popular hypothesis is that the basal ganglia contribute to the organization of individual elements into a sequence and the automaticity with which those actions are performed. Anterior regions of the putamen have been found to be active

during the planning period before the first element of a sequence is initiated (43, 98, 204). Additionally, while mice learned to execute a sequence of lever presses, some neurons in the basal ganglia were observed to increase or decrease their firing rate at the beginning of the lever press sequence as if they signaled the initiation of a chunk of actions, while other neurons were excited throughout the entire sequence of lever presses (210, 211). It is unclear, however, whether the basal ganglia actually represent the learned sequence of presses or if this activity simply signaled the onset of a movement period that was expected to ultimately give rise to a reward, since the mice did not appear to have perfected execution of the four-press sequence. On the other hand, the basal ganglia has been implicated in gating individual actions to regulate their order (39), suggesting that the basal ganglia may control the outflow of an action sequence that is determined elsewhere rather than actually storing or driving execution of the entire sequence.

Our understanding of the role of the basal ganglia in sequence learning has been complicated by findings from neuropsychological studies [see (88) for review]. These studies in large part suggest that explicit sequence learning ability is preserved in patients despite having basal ganglia impairments. For example, the ability to execute sequences correlates with severity of symptoms of Parkinson's disease, but not with other measures such as cognitive impairments or amount of dopaminergic medication (311). Patients with Parkinson's or Huntington's disease are also able to verbalize a learned sequence explicitly, despite having difficulty executing it (90, 435). Finally, patients exhibit generalization of learned sequences to the opposite hand (14). Together these data suggest that explicit sequence learning remains intact despite disruption to the basal ganglia. What remains unclear, then, is why these patients should exhibit sequence-learning impairments at all (401). One hint comes from the finding that these patients perform worse compared to controls on a probabilistic sequence task that probes statistical learning (460). Thus, to the extent that there is any implicit learning occurring in sequence-learning tasks, the basal ganglia may be important for that process. Alternatively, basal-ganglia impairments may lead to a failure to automatize explicitly learned sequence orders, giving rise to difficulty in the maintenance and automatic execution of whole sequences, or they may simply regulate the outflow of sequence elements according to an order stored elsewhere, potentially in an explicit manner. Indeed, a study in monkeys calls into question whether the basal ganglia play a role in the execution and storage of motor sequences (78).

The role of the basal ganglia in sequence learning *per se* is further called into question by the fact that the basal ganglia are known to mediate intrinsic motivational state (284) and knowledge of sequence order leads to sequence-specific performance improvements by increasing motivation (474). Hence, it remains possible that an apparent role for the basal ganglia in learning and producing sequences may be confounded with motivational effects on execution.

The hippocampus supports fragmentary knowledge of sequence order

It was originally believed that the hippocampus does not participate in sequence learning, on the basis of studies investigating sequence learning ability in patients with amnesia (74, 322, 324, 351, 352). However, more recent evidence from neuroimaging studies has suggested that the hippocampus is active not only when participants are explicitly aware of the presence of a sequence, but also when participants are not informed that a sequence exists (108, 376). In general, activation of the hippocampus is observed to decrease as the sequence is learned (108, 136, 357, 376), although its strength of activation during learning correlates with the magnitude of offline gains that occur following consolidation (8, 9).

Evidence from these studies suggest that the role of the hippocampus is likely to be in supporting the learning of associations between nearby (e.g., first or second order) stimuli; that is, in acquiring knowledge of sequence fragments. This knowledge can then become automatized, and less declarative, which could explain the gradual decrease in hippocampal activity observed as learning progresses. In line with this hypothesis, it has been demonstrated that the hippocampus is more active when learning perceptual sequences, which are likely more declarative (362). Additionally, the hippocampus is more active for sequences that require knowledge of higher-order associations (e.g., second-order sequences in which it is necessary to know the prior two elements to predict the next upcoming element, rather than simple pairwise associations) (74, 376). Finally, there is some evidence that activity in the hippocampus actually increases very early in learning (108, 127), again suggesting its importance in associating small numbers of sequence elements together explicitly. Thus, the hippocampus appears to contribute to sequence learning by supporting the acquisition of fragmentary sequential orders, which can then be chunked and consolidated into higher-order sequence representations.

Learning-related activity in frontal regions

Another region that has received a lot of attention in sequence learning is the supplementary motor area (SMA). Activity in SMA tends to change as sequence learning proceeds (258). Moreover, SMA is active during the planning period prior to the execution of a sequence (43, 98); thus, SMA is thought to have a significant role in the planning and control of movement sequences. In line with this, rTMS over SMA interferes with the ability to accurately perform complex sequential keypresses (125). Additionally, SMA has been implicated in performance of both saccadic and arm or finger sequences (123, 206, 257, 308, 396), arguing that it serves an effector-independent role in representing sequences. Finally, neural activity in SMA appears to be sequence-specific; neurons respond to particular actions only when they exist at particular positions within a sequence (308), suggesting its role in maintaining a sequence-order representation.

At the most anterior region of SMA is the pre-supplementary motor area (preSMA). Unlike the SMA proper, preSMA primarily projects forward to prefrontal areas (27, 266, 431) rather than projecting back to primary motor cortex or to spinal cord (95, 164, 266, 280, 431). preSMA tends to be most active during the learning phase (176, 177, 314, 370) such as by responding before each chunk of the sequence in an $n \times m$ task (175), but is less active once the sequence has been learned (e.g., firing only before the entire hyperset but no longer firing between chunks). In fact, inactivation of preSMA causes increased errors when performing novel sequences but has no impact on the execution of learned sequences (314). In contrast, SMA is equally or more active during performance of sequences that have already been learned compared to during learning (176, 177, 314).

On a finer-grain scale, neural recordings have suggested that SMA appears to encode the preparation of the next movement to be executed (11, 254, 420), since activity reflecting, for example, the second action in the sequence gradually increases from the start of the sequence until the point when the second element is to be executed (313). In contrast, neural activity in preSMA is modulated by the ordinal position of a particular action within the movement sequence (198); for example, neurons may respond to the second action during sequence planning but their activity declines even before the first sequence element has been completed (313). This suggests that preSMA either serves as a memory buffer for future actions in the sequence, or it assists in maintaining the proper order of the sequence elements to be executed—both particularly important for learning a sequence.

Neural activity within other frontal regions also has been suggested to relate to sequence learning; however, these contributions likely have little to do with motor learning. For example, neurons in prefrontal cortex that fire just prior to the execution of a particular element of a sequence also fire during the preparatory period before any of the sequence has been executed: during the preparatory period, prefrontal cortex appears to simultaneously reflect all of the future sequence elements that will be subsequently performed (309). Thus frontal regions including SMA represent the order of the whole sequence or of sequence chunks, which can in turn be used to guide the execution of that sequence by motor cortex element by element.

Summary: Sequence learning

Much effort has been focused on understanding how sequences of discrete actions are learned. Sequence-learning paradigms have provided a window into the manner in which existing movement abilities can become organized in a specific order [largely affecting goal selection (Fig. 1)], how the brain may form compact cognitive representations to chunk together groups of ordered actions, and how the brain uncovers statistical regularities in the environment. It remains unclear, however, how this work advances knowledge about learning to execute complex continuous sequential

actions like a tennis serve or the sequence of muscle activations required for a simple reaching movement—the types of behaviors that frequently inspire investigations into sequence learning in the first place. Even in the case of fast sequencing of fingers on a keyboard, in which individuals learn to eliminate any discrete intervals between the end of one finger movement and the start of another, it is not clear that there is more to these behaviors than the combination of knowledge of the sequence order (which can become automatized and implicit, and may become compactly represented as chunks) and the ability to quickly select and perform the individual finger-movement elements; there currently exists no evidence for a contribution of learning to better execute specific transitions between fingers. Instead, sequence tasks primarily inform us about the manner in which overlearned movements can be rapidly selected for execution in the appropriate order, such as rapidly typing one's ATM number.

Sequence learning therefore remains a somewhat unsatisfactory model for learning of continuous motor skills. The motor execution component in these tasks is, for the most part, trivial or is already well learned. It is also challenging to disambiguate the combination of explicit and implicit knowledge that contributes to sequence learning; thus, the extent to which sequence learning speaks to motor skill learning as opposed to the cognitive learning of order remains unclear. While the rapid action selection that emerges in sequence learning is undoubtedly an important aspect of motor learning in general, we suggest that there are alternative paradigms that better isolate this aspect of learning—which we discuss in the section on “*De Novo Learning*.”

Motor Skill: *De Novo Learning*

As we discussed in the section on adaptation, in some scenarios motor learning requires us to adjust existing actions in such a way as to recover performance of a previously mastered skill. However, in most cases, acquiring a new skill requires us to learn new ways to respond to incoming information by selecting the appropriate action response, whether that is information coming from the environment (e.g., the target has moved) or from sensors within our body (e.g., my arm is not where I expected it would be). In other words, we are often required to learn a novel feedback controller from scratch that changes how our actions are selected and executed, often according to a particular task context (i.e., goal). Importantly, this poses a very different challenge to acquiring skills by adapting or repurposing an existing skill, for example, learning to use a tennis racket when one has already learned to use a squash racket. Instead, it is necessary to assemble a brand new skill *de novo*.

In the previous sections describing adaptation and sequence learning, we have seen how the brain brings many learning mechanisms to bear on the problem. These processes, which, for instance, include explicit learning, are often viewed as contaminants to our attempts to assess implicit adaptation

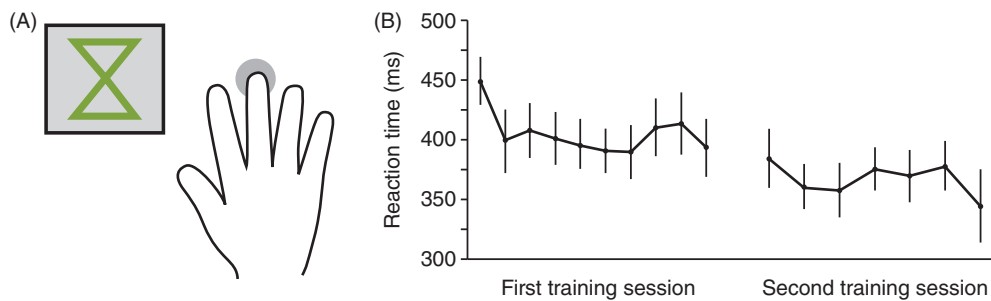


Figure 14 Arbitrary visuomotor association learning. (A) In (21), participants were required to associate a set of visual stimuli with specific finger presses. (B) Although the basic mapping was learned quickly, with practice, participants were able to reduce the reaction time needed to generate the correct response. Adapted from (21); republished with permission of the Society for Neuroscience, permission conveyed through Copyright Clearance Center, Inc.

or implicit learning of a movement sequence. We suggest that many of these “contaminating” processes in adaptation and sequence learning tasks are those which support the capacity to learn entirely new and arbitrary policies. In this section, we review paradigms that allow these processes to be studied in isolation, without contamination by processes such as statistical learning and implicit recalibration.

Learning arbitrary visuomotor associations (AVMA)

In the simplest paradigm for investigating learning *de novo*, subjects must learn an arbitrary association between a discrete set of stimuli and a discrete set of actions (Fig. 14). For instance, participants may learn to associate each of four visual stimuli—perhaps colors or shapes—with each of four different buttons on a keyboard. Performance in this task can be assessed in two ways: either based on proportion of responses that are accurate, or based on the speed of responses (i.e., reaction time). More generally, performance level can be assessed based on the speed-accuracy trade-off, that is, how accuracy varies as a function of response time (157,456).

Learning in this paradigm occurs in two distinct phases. First, participants learn the association between stimuli and actions. Depending on the number of associations to be learned, this phase tends to proceed quite rapidly. It is known to be highly cognitive and is dependent on the hippocampus, premotor cortex, and parietal cortex (468). However, although performance can be accurate at this stage, it is typically slow. In the second phase of learning, participants practice the identified association, which leads to them being able to perform the association at lower latency, while being less susceptible to inference by a concurrently performed secondary task.

A consistent debate has been whether such learning is truly visuomotor in nature, or merely visuospatial. That is, do participants genuinely learn a mapping between visual stimuli and actions (visuomotor), or do they learn a correspondence between visual stimuli and spatial goals for movement (visuospatial)? This seems to vary according to the task. In cases where a set of visual stimuli are associated with arbitrary

gestures, patients with lesions to premotor cortex are unable to learn the association, despite being able to successfully produce each individual gesture through imitation. The same patients, however, were relatively unimpaired when similar stimuli were associated with pointing movements toward different targets (154). Thus, premotor cortex seems to be necessary for learning pure visuomotor associations. Visuospatial associations, however, can be learned independently of premotor cortex. When a given task could be learned either as a visuospatial or as a visuomotor association, visuospatial associations seem to be favored. This dominance of visuospatial learning is further supported by a study by Grol and colleagues (140). They trained participants on a simple association between images and finger presses. After this initial learning session, participants’ hands were pronated by 180°, and the symbol-key bindings were modified such that either the fingers which needed to be pressed remained the same, but the spatial location of the required keys was reversed, or the key locations remained the same but had to be pushed with a different finger. Participants coped better with this postural adjustment when the spatial location of the required key was preserved, rather than when the required finger was preserved, suggesting they had represented the original task visuospatially.

The amount of training provided to participants in arbitrary visuomotor association tasks varies widely. Many studies examine learning only within a single session, while other studies track learning over much longer timescales. Even with relatively simple associations, comprising just two to three elements, reaction times can continue to improve over multiple days of practice (21, 139). Decreasing reaction time is not the only way in which performance improves; practice also leads to a reduction in the cognitive load associated with the task. Shortly after learning a novel association, participants struggle to concurrently perform a cognitively demanding secondary task (such as counting the number of vowels among a sequence of auditory stimuli). Typically, however, after around two to five days of practice (depending on the tasks) they learn to perform both the association task and the

secondary task without compromising performance in either one (21, 139, 480).

Many of the phenomena observed in arbitrary visuomotor associations is similar to what has been established in sequence learning: practice leads to faster, more automatic responding. Sequence learning can even be considered a variant of arbitrary association learning in which the cue is not a visual stimulus but the preceding movement. Thus, the AVMA paradigm likely captures the same salient features that are of interest in highly practiced sequence tasks. Where these tasks differ is that sequence learning involves the added complexity of working memory constraints and chunking—that is, they differ in the initial cognitive mechanisms of acquisition. Thus, although AVMA learning shares many of the limitations of sequence learning—for instance, execution of individual movements does not improve—it arguably offers a more streamlined paradigm in which to study motor-specific aspects of learning, namely the ability to rapidly generate appropriate motor output in response to specific events or stimuli.

Also related to arbitrary visuomotor association learning is the problem of category learning. Category learning typically involves learning a rule or mapping assigning different stimuli to two or more different categories, much like we can easily categorize images of cats versus dogs. Whereas AVMA tasks draw from a finite number of stimuli, category-learning tasks typically draw stimuli from a continuous space, with a predefined boundary determining category membership. For instance, the stimuli may be Gabor patches with differing frequencies and differing orientations, and the membership boundary might depend on both of these features. Although category learning is often regarded as a perceptual problem, categorization decisions are typically expressed through movement, for example, pushing one of two different buttons. Extensive training in categorization tasks often ends up resembling learning of a stimulus-to-action policy, as evidenced by the fact that switching the buttons after the task has been well-learned leads to persistent performance difficulties (16, 167, 268). It is likely that category-learning tasks engage very similar learning mechanisms to arbitrary visuomotor association learning, only with the added complexity that the extent of cognitive involvement can depend on how complex the decision boundary is (17).

Many brain regions have been implicated in learning arbitrary visuomotor associations. Lesion studies in humans and non-human primates have implicated the hippocampus, prefrontal cortex, cerebellum, and the basal ganglia in initial acquisition of arbitrary associations (468). The neural correlates of long-term practice in these tasks are less clear. However, it has been suggested that overlearning of visuomotor associations might reflect the emergence of novel stimulus-response representations in the parietal cortex (139) and/or the cerebellum (21), a shift to being represented within different subregions of the striatum (15), or cortical computations becoming independent of the striatum (166).

Learning of arbitrary continuous skills

Arbitrary associations between discrete sets of stimuli and actions provide an elementary model of feedback learning. Most real-world skills, however, are more complex and range from generating sequences of actions over time to maneuvering an object toward a desired goal. The relationship between actions and their effects on the state of the world can often be entirely arbitrary. For instance, when driving a car, pressing one pedal to accelerate the car, and pressing an adjacent pedal to slow it down, is an entirely arbitrary control interface. Changing the heading angle of the car using hand movements on a steering wheel is also a very unnatural control mechanism. We nevertheless master these types of control and employ them effortlessly given sufficient instruction and practice.

Adaptation tasks do not model this type of learning well because they permit participants to learn by repurposing or adapting existing controllers; thus these paradigms largely influence action selection but not action execution. In contrast, *de novo* learning of continuous skills also requires that individuals not only rapidly select a new response, but also execute those responses well. As we have discussed in the section on adaptation, the hallmark of adaptation is the existence of aftereffects—the original skill that was adapted or repurposed inevitably suffers when we attempt to revert to it. With *de novo* skill learning, by contrast, the new policy is assembled from scratch, without interfering with pre-existing controllers. Consequently, it should be much easier to disengage a *de novo* learned controller and return to using a baseline controller without experiencing unwanted aftereffects.

A simple task that does not seem to be able to be solved through implicit adaptation is the mirror-reversal paradigm (Fig. 15), in which the visual field is inverted across a mirroring axis. This type of extreme perturbation can be achieved with motion tracking and a visual display, or by using special prism goggles (133). A recent study by Telgen and colleagues (426) highlighted a fundamental difference between how a mirror-reversal is learned compared to a visuomotor rotation. Critically, although participants responded well to the mirror-reversal or the rotation when given sufficient time to act, when they were forced to respond rapidly (prompted by an unexpected cursor jump mid-movement [Fig. 15C]), the initial corrective response was the same as at baseline—not in the appropriate, mirror-reversed direction (Fig. 15D). Therefore, learning of the mirror-reversal was not expressed at low reaction times [see also (138, 223)]. By contrast, it is known that implicit recalibration, such as under an imposed visuomotor rotation, is reflected in rapid feedback responses (6, 64, 426). This difference suggests that these two perturbations were learned via different mechanisms—presumably, adaptation in the case of a rotation, and *de novo* learning in the case of the mirror reversal. The longer time required to generate appropriate movements under a mirror-reversal suggests reliance on a cognitive mechanism. This cognitive component is likely

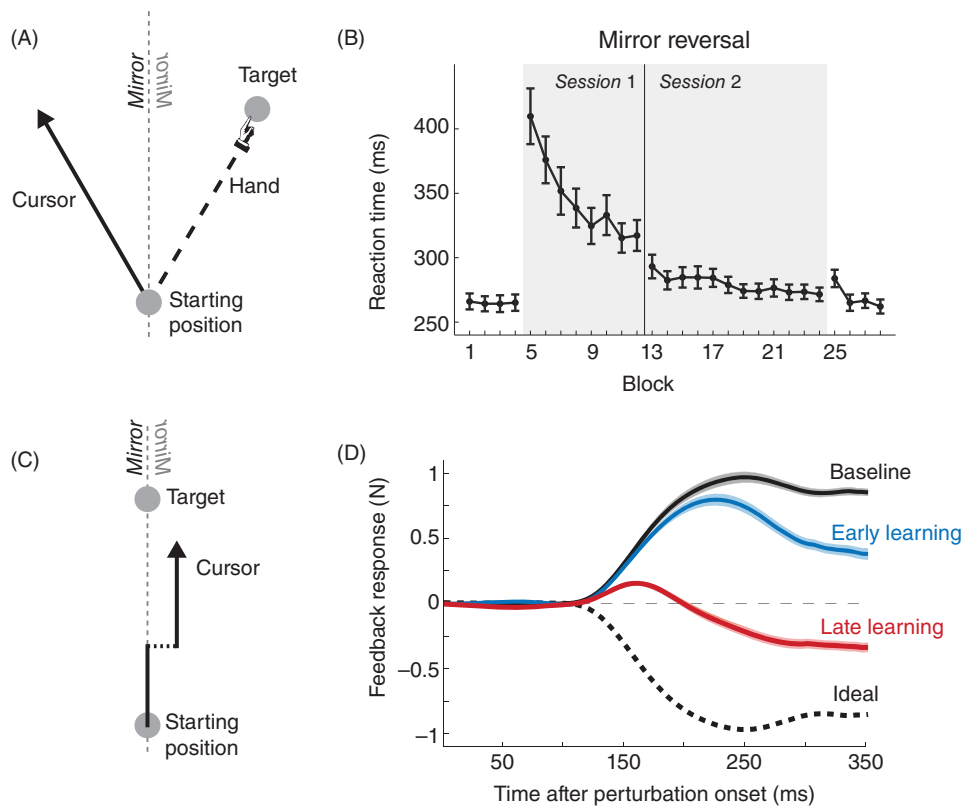


Figure 15 Mirror reversal learning. (A) Mirror-reversal task in which cursor motion is reflected across a mirroring axis. (B) Practice enables accurate compensation to be achieved at lower and lower reaction times. (C) Feedback responses can be assessed by displacing the cursor midway through a movement toward a target positioned on the midline. (D) Responses to target displacement early in learning (blue; when movements are accurate, but require long reaction times) are similar to baseline (nonmirrored) responses (black), rather than ideal responses (dashed black). Even after 2 days of practice, responses fail to be appropriate for the mirror-reversal and are initially directed in the wrong direction (red). Adapted from (426); republished with permission of the Society for Neuroscience, permission conveyed through Copyright Clearance Center, Inc.

qualitatively similar to explicit components that contribute to learning in adaptation paradigms, which are known to be similarly time consuming (105, 149, 259) [in contrast to implicit recalibration, which can be rapidly expressed (149,426)]. This initial cognitive phase parallels that occurring during learning of an arbitrary visuomotor association. It is tempting to speculate that further practice would ultimately allow appropriate feedback corrections to be generated at low latency in the mirror-reversed condition; however, feedback responses under mirror-reversal remain deficient even after 8 days of continual exposure to reversing prism goggles (262). The fundamental difference between learning to compensate for mirror reversals compared to small rotations is underscored by neurological dissociations. Patients with Parkinson's disease and Huntington's disease appear normal in their ability to compensate for displacing prism goggles or for visuomotor rotations (30, 143, 260, 272); however these patients are strikingly unable to compensate for mirror-reversed feedback in a throwing task (143), suggesting a critical role for the basal ganglia in *de novo* learning.

Related to mirror reversals are more extreme perturbations such as 180° rotations. These extreme rotations are too large to be solved by implicit recalibration, which, as we discussed in the section on motor adaptation, seems to be limited to compensating for relatively small ($<25^\circ$) perturbations (44, 301, 302). Indeed, it has often been noted that the nature of compensation for a visuomotor rotation changes qualitatively as the size of the rotation increases (2,301). 180° rotations actually arise naturally in many real-world tasks via the fulcrum effect: when trying to manipulate the tip of a tool that is fixed somewhere along its axis, the movements of the tip of the tool will be rotated by 180° relative to movements of the hand. This difficulty occurs, for example, in laparoscopic surgery (118), and can require substantial practice to master (71).

In mirror-reversal learning, and in learning to counter extreme rotations, the relationship between actions and outcomes can be easily described to and understood by participants, which may aid performance. Indeed, participants cope significantly better with mirror-reversed cursor feedback if the

display depicts the mirror-reversal as arising from a simple fulcrum (28). In mirror reversal, the newly learned action to reach a target conflicts with baseline actions perpendicular to the mirroring axis but is congruent to baseline actions along the mirroring axis. This is very different from the scenario that occurs when using thumb movements to play a video game or arm movements to steer a bicycle: in those cases, the underlying novel mappings are neither in conflict nor in congruence with any pre-existing ones. It can therefore be difficult to interpret whether difficulty learning a mirror-reversal is attributable to learning *per se*, or to resolving this conflict.

A number of other paradigms have challenged participants to learn more complex, arbitrary mappings from actions to outcomes. One example is the use of myoelectric interfaces, in which activity of muscles, measured via EMG, is used to control an on-screen cursor. The normal use of arm muscles to control the arm naturally gives rise to a mapping from muscle activity to a spatial location. It is possible to have human participants control the location of an on-screen cursor directly based on their muscle activity by simulating this mapping from muscle activity to effector location (348, 365). The myoelectric interface, however, allows various distortions to be simulated, such as weakening of a muscle. Much like in a visuomotor rotation paradigm, participants appear to compensate for these relatively minor perturbations by learning to re-aim the cursor toward an alternative target (365). However, this strategy is no longer possible in more extreme cases; randomly permuting the roles of all the muscles involved gives rise to a complex EMG-to-cursor mapping that cannot be solved by adjusting pre-existing controllers. Instead, it requires a change in which muscles are selected to perform each action. These tasks subsequently require a honing of movement accuracy by improving execution of the selected actions. Thus given time, participants can learn to successfully maneuver the cursor around the screen to navigate between targets (348), demonstrating the flexible capabilities of *de novo* learning. Another example is the use of a cyberglove interface to control an on-screen cursor (Fig. 16). Mosier and colleagues (304) used a cyberglove to record the posture of the hand—a total of 19 degrees of freedom. These 19 degrees of freedom were mapped linearly onto a cursor

location on a 2-d screen. Participants learned to control a cursor using this mapping over two to three sessions of practice.

Although it is unclear exactly how *de novo* tasks are learned, there is likely to be a substantial cognitive component. The control solution that participants acquire depends strongly on the type of visual feedback they are provided. If participants are shown only a cursor moving on a screen, they learn to move the cursor along straight lines on the screen (304). If, by contrast, the cursor is represented as the endpoint of a simple two-link arm, participants learn to move the cursor in a way that minimizes distance in terms of the changes in joint angles of the two-link arm, despite the fact that the mapping between hand posture and the cursor is identical in either case (76). Thus, the control solution that participants arrive at depends critically on how they cognitively conceive the task.

An extreme example of a *de novo* learning task was developed by Fells and Hinton (102), in which both hand movements and hand posture were used to adjust the characteristics of an auditory tone. Through careful and precise movements, it was possible to richly modulate the tone to generate speech-like sounds. With sufficient practice, an expert user could conduct full conversations using the glove. This complex and arbitrary motor-to-auditory mapping was initially developed as a tool to enable speech synthesis in persons otherwise unable to speak. However, it beautifully demonstrates both the kinds of complex, arbitrary skills that people are capable of learning, as well as the complexity of speech itself.

De novo learning tasks need not be high dimensional to be challenging to learn. An experiment by Roland Johansson and colleagues (212) required participants to control a 2-d cursor through a combination of squeezing or twisting a purpose-built manipulandum. The participants showed a similar learning pattern of slowly converging on the ability to maneuver the cursor in straight lines. Furthermore, participants were able to learn two variations of this mapping in parallel, with the second mapping corresponding to a 180° rotation applied on top of the first mapping. Participants could easily switch between these mappings, providing further evidence that the mappings were learned by constructing a new controller in each case rather than by updating existing controllers.

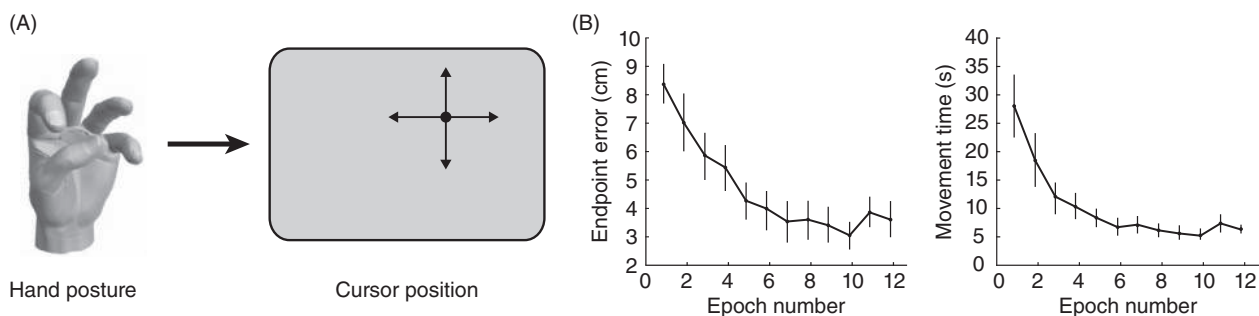


Figure 16 A complex *de novo* learning task. (A) Hand posture is mapped onto a 2-d cursor position. (B) Initially, participants are unable to effectively control the cursor but, with practice, become able to generate smooth, straight cursor trajectories. Adapted from (76); republished with permission of the Society for Neuroscience, permission conveyed through Copyright Clearance Center, Inc.

De novo learning of an arbitrary controller is also observable in brain-machine interfaces (BMIs). Typically, these devices extract a set of neural firing rates from an implanted electrode, and use these activities to control an on-screen cursor. A lot of work using brain-machine interfaces has attempted to leverage “natural” patterns of brain activity to achieve this, by identifying the patterns of neural activity that a monkey uses to move its own hand, then using this to decode activity after the hand is immobilized to drive movement of an on-screen cursor or a robot arm. Errors in the decoding process can be corrected using adaptive brain-machine interfaces (391). It is also widely recognized, however, that successful operation of a BMI device very much depends on learning on the part of the subject also. As much as a decoder can be adjusted to improve performance, the subject can learn to adjust their control of the device—a process that often improves incrementally over several days (121). Brain-machine interfaces have thus emerged as an important experimental tool for probing the characteristics of motor learning (122, 132).

Recent work has suggested potential constraints on what kinds of mappings can be learned *de novo*. In a BMI paradigm in monkeys, Sadtler and colleagues (368) applied different mappings from neural activity to cursor kinematics. The difficulty of learning to control the cursor location depended on whether or not the required neural activity tended to occur during natural behavior. If the required activity pattern was part of the monkey’s neural “repertoire” and simply had to be generated under different circumstances than usual, the monkey could learn to control the cursor relatively quickly. If, however, the interface required activity patterns that the monkey did not normally generate, learning was much slower and less complete. This finding illustrates the fact that *de novo* learning can encompass at least two distinct processes: (i) learning to select an existing action under different circumstances than before, and (ii) broadening the repertoire of available actions.

Relatively little is known about the neural basis of *de novo* skill learning compared to other forms of learning. As discussed, studies on neurological patients have highlighted the importance of the basal ganglia in this kind of learning. Learning of a simple form of BMI control has also been investigated in mice. Koralek and colleagues (242) trained mice to use a neuroprosthetic device, which mapped activity of a small group of neurons to the pitch of an auditory tone. The mice learned to control this pitch to obtain food rewards. This learning process was found to depend critically on corticostriatal plasticity. Interestingly, the exact location of the neurons used to control the auditory cue did not seem to be important; mice were equally capable of controlling the tone using neurons in sensory cortex as they were using neurons in motor areas (62). As these types of paradigms continue to be explored, we may gain a better understanding of the neural circuits that uniquely govern *de novo* learning in contrast to other forms of motor learning.

Motor Skill: Motor Acuity

In the previous sections, we have described various paradigms that primarily require learning of which action should be selected: for example, to counter a systematic perturbation, for insertion into a particular sequence order, or through association with a specific stimulus. In the final section of this review, we focus on how an action, once selected, can be executed with more accuracy and precision through practice. This kind of motor learning has been much less studied in humans than in animals. We will therefore begin by describing work in non-human animals, which consequently means that there will be more detail at the neural level than was described in previous sections.

In the animal literature, motor-skill learning has mainly been studied using prehension tasks (reaching and grasping). Performance in these tasks can be quantified with either a global measure of task success or with respect to movement kinematics, with an emphasis on speed, accuracy (mean error), precision (variable error), trajectory smoothness, and trajectory stereotypy. In the rodent, a widely used task trains the animal to reach through an aperture to grab a pellet off a shelf or grasp a piece of pasta (Fig. 17A-D) (12, 454). In monkeys, precision grip is trained by having the monkey remove food pellets from food wells (Fig. 17E-J) (327, 328). In both tasks, difficulty is progressively titrated by moving the pellet further away in the rodent case, or decreasing the diameter of the food well in the monkey case. Acuity improvements are not limited to grasping, however; a seminal study in monkeys tracked changes in planar reaching trajectories over about a month of training and found that they became less dispersed (more stereotypical) over time (124). Overall, however, behavioral studies that have placed an emphasis on quantifying learning-related changes in the kinematics of continuous movements are surprisingly rare.

There are several reasons for the relative paucity of studies that examine improvements in motor execution. First, as we mention in the introduction, motor learning has largely been studied from the standpoint of improvement at selecting the right action (e.g., its direction, amplitude, or order in a sequence) rather than changing the quality of action execution (e.g., reductions in variability). Second, a great advantage of rodent and non-human primate work is the variety of new tools that have become available to study learning-induced changes in neural circuit structure and activity. Thus, the majority of the work in animal models has focused on neural substrate and has rested on the assumption that measures at the level of task success will suffice as a correlate of the quality of movement execution. Third, many studies have employed sequence-learning paradigms to study execution components of motor skill learning (210, 246, 458). However, as we have argued in the section on sequence learning, such tasks do not provide a good model of the motor-execution components of skill learning.

The lack of fine-grained behavioral analysis of prehension skill in animal models raises an important problem: more

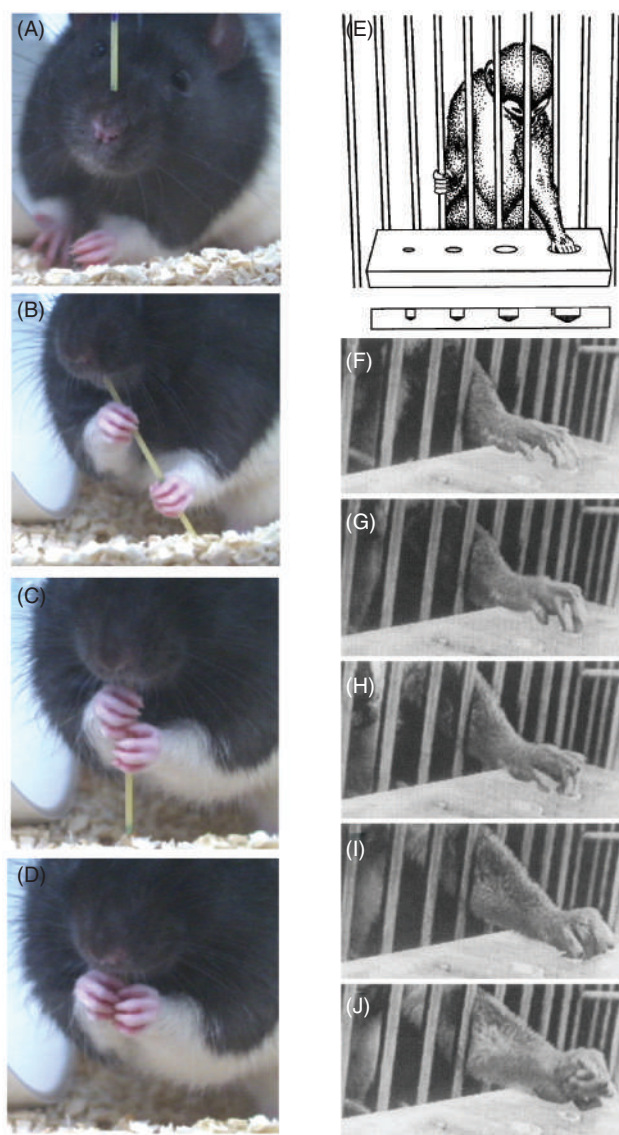


Figure 17 Examples of prehension tasks. (A–D) Vermicelli handling task [adapted, with permission, from (12), Fig. 1]. A sequence of snapshots showing the task during one trial, from (A) the vermicelli piece being dropped into a conveniently viewed part of the cage, (B) the rat begins eating using an asymmetrical holding pattern, with the two paws designated as “grasp” and “guide” ones, to (C and D) the two paws moving together as the piece becomes shorter and digits become interposed. (E) Food pellet retrieval task [adapted, with permission, from (327), Fig. 1]. Monkeys retrieve a food-pellet from the apparatus, Plexiglas board (Klüver board) containing four small food wells with sizes ranging from 9.5 to 25 mm. (F–J) A sequence of snapshots showing a monkey retrieving a food pellet [with permission from (328), Fig. 2]: (F) finger extension, (G) finger flexion, (H) finger flexion + wrist extension, (I) wrist extension, and (J) Forearm supination. Panels (E) and (F–J) republished with permission of the Society for Neuroscience from (327) and (328), respectively; permission conveyed through Copyright Clearance Center, Inc.

global measures do not precisely characterize the basis of performance improvements. For example, improvements in overall task success could be due to reduction in mean error or a reduction in movement variability. This consequently makes it very difficult to interpret anatomical and physiological

changes associated with improvements in global performance measures. Even once the right behavioral variable has been identified, the observed changes in neural circuits may correlate with the changes in behavioral components but do not necessarily *explain* how those changes were achieved.

Despite these caveats, rodent studies of prehension training have yielded much important information in recent years. In particular, they make a good case that motor skill learning is causally related to structural and physiological changes in motor cortical areas. Early experiments in the rat showed training-related increases in dendritic branching (arborization) in both layer II–III and layer V of motor cortical neurons contralateral to the reaching paw (124, 238, 469). Since these early studies, it has been shown that these changes are transient, with a return to normal dendritic tree size, but without concomitant loss of the skill itself (340). This implies that increases in dendritic arborization are a marker of the learning process but are not themselves the cause of the improved performance. A clue to what the skill trace might actually be has come with the advent of studies using longitudinal two-photon microscopy in mouse models, showing selective turnover of individual spines on the dendrites of neurons that project to the spinal cord (which are therefore considered movement-relevant) over the course of motor learning. Specifically, new spines are formed and retained, whereas an approximately equal number of old ones are eliminated, keeping the total number the same. Interestingly, some of the spines that are eliminated correspond to inputs from inhibitory interneurons (59), which is consistent with physiology that suggests changes in cortical inhibitory/excitatory balance with skill learning (340).

How should this exciting new work be interpreted? One interpretation has been to simply conclude, assuming that spines are proxies for synapses, that “motor skill learning relies on the formation and selective maintenance of new synapses within the motor cortex” (340). There is something a bit unsatisfying about this conclusion, however, because we are still left with the question of where is the whole motor skill stored after learning? The very same question has been asked, and partially answered, in mouse studies of memory engrams (346). Specifically, it has now been shown in the mouse that increases in spine density and increases in strength at individual synapses of memory-relevant cells are *not* the mechanism of memory storage. Rather, what seems to matter is the *pattern* of connectivity within an ensemble of cells. Indeed, in a revelatory experiment, weakening of synaptic connections between the cells in a particular hippocampal ensemble failed to abolish a specific memory, as it could still be retrieved by direct optogenetic stimulation; that is, the ensemble’s pattern of connections was intact even if the strength of the connections was altered (367).

The distinction between the *pattern* of connections between the cells in an ensemble and the *strength* of these connections is likely to generalize to the case of motor-skill learning and representation in motor cortex. In the case of skilled prehension, primary motor cortex—the area that is

thought to be responsible for movement execution—is also the locus for learning. This is not true for the prefrontal cortex, basal ganglia and cerebellum, which are areas correlated with motor learning by instruction, reward, and error, respectively, but are not the origins of the motor commands that express what has been learned in the moving limb (at least in primates). One explanation as to why primary motor cortex, and not other structures, is so important for such skills is that improved skill requires the proper coordination of *new* combinations of muscle activations; as the motor cortex controls muscles and forces, alterations supporting improvements in skill must take place there. It is also intuitively appealing to consider such combinations (or synergies) to emerge from the pattern of connectivity from the cortex to descending pathways (329).

A lot is left out of this necessarily short and corticocentric account of how motor skill execution can be improved through practice. The importance of the inputs to motor cortex and the type of output it has available to access the spinal cord will also likely determine the degree of skill that can be developed in any given species. In a fascinating example of this, it was shown in a recent study that postnatal mice transiently possess direct cortico-motorneuronal connections but these are then eliminated. If this developmental elimination is prevented, then the adults have markedly enhanced manual dexterity compared to normal adult mice (141).

Many physiological studies of motor-skill learning have placed an emphasis on changes in motor-cortical maps. Such maps are constructed by applying a low-intensity current pulse through a microelectrode at successive contiguous sites, and seeing which effector this causes to move. Studies have shown that training on prehension tasks leads to expansion of territory of the trained effector in motor cortical areas (233, 328). Critically, however, the persistence of this expansion is not necessary for retaining the motor skill (234, 300, 427)—an observation that can be considered a physiological analog of the normalization of dendritic arborization and spine density discussed earlier. Overall, these studies of motor skill learning suggest that the neural processes that operate in motor cortex during the formation of a motor skill are different from those that allow its retention and expression. A stark demonstration of this separation was made in a study of motor-skill learning in rats that demonstrated the necessity of dopaminergic projections to motor cortex from the ventral tegmental area during skill acquisition; however, lesioning these projections had no detrimental effect on performance once these skills had been acquired (182).

What about skilled prehension in humans? Surprisingly, studies of improvements in reaching and grasping are almost nonexistent. As we state in the introduction, the vast majority of motor learning studies, particularly in humans, have focused on either adaptation or sequence learning—paradigms that do not challenge motor execution, but rather stress the need for rapid selection of movements that can already be executed at ceiling levels. In support of this assertion, a recent meta-analysis of 70 imaging studies of motor

learning in humans concluded that there was no converging evidence for learning-related activation changes in contralateral M1 (158). Clearly, one does not want to conclude that humans do not need their primary motor cortex for expression of motor skills but rather that learning of motor acuity is either little studied or challenged by the adaptation and sequence-learning tasks that dominated this meta-analysis. This conclusion in regard to sequence learning is supported by a very recent study showing that even after 5 days of intense practice in a finger sequencing task, there was little or no evidence for a true sequence representation in M1, that is, M1 was not making a *new* learned contribution to the task (484). Thus, there are few human data that can be directly compared to the rodent and non-human primate work on skilled prehension discussed above.

A few paradigms have examined reduced variability of movement in more abstract tasks. In a “skittles” paradigm, participants had to “throw” a virtual ball on a string in such a way that it knocked over a skittles while avoiding an intervening obstacle (306, 307). The position and velocity of the hand at the time of releasing the ball fully determines the outcome of this task, and a particular subset positions and velocities will be successful. Initially, participants had quite variable and inaccurate release kinematics but, with practice, appropriately tuned their mean release state, reduced the variability, and finally shaped their variability such that the dimensions along which variability was greatest had little impact on task performance. One caveat to this work, however, is that it is unclear how much of the variability reduction is associated with improved capability of executing the correct actions through a later stage exploitation of the identified solution, and how much of it is associated with initial, highly variable exploration of the task space.

A recent study attempted to isolate acuity improvements in execution through a task that required subjects to make visually guided, continuous curved movements of the wrist to guide a cursor through a U-shaped tube (arc-pointing task, Fig. 18) (398). The movements were made to be curved for two reasons. First, point-to-point reaching movements are so well practiced in humans that they have limited dynamic range for capturing practice effects across days. Second, the curved movements required a sequence of joined submovements and continuous feedback adjustments to navigate the tube. Thus one could consider this task to be like a tennis serve or throwing action—more difficult but nevertheless continuous. Participants practiced the arc-pointing task across five days. Motor-skill learning was assessed at both the level of task success, defined as a shift in the speed-accuracy trade-off function (SAF), and at the level of trajectory kinematics. Improved performance at the task level was mainly attributable to reductions in trial-to-trial trajectory variability, with minimal changes in the mean. The term “motor acuity” was coined to capture this reduction in movement variability. Interestingly, the number of submovements remained invariant, which speaks against chunking at the motor level for continuous skill tasks. There was also

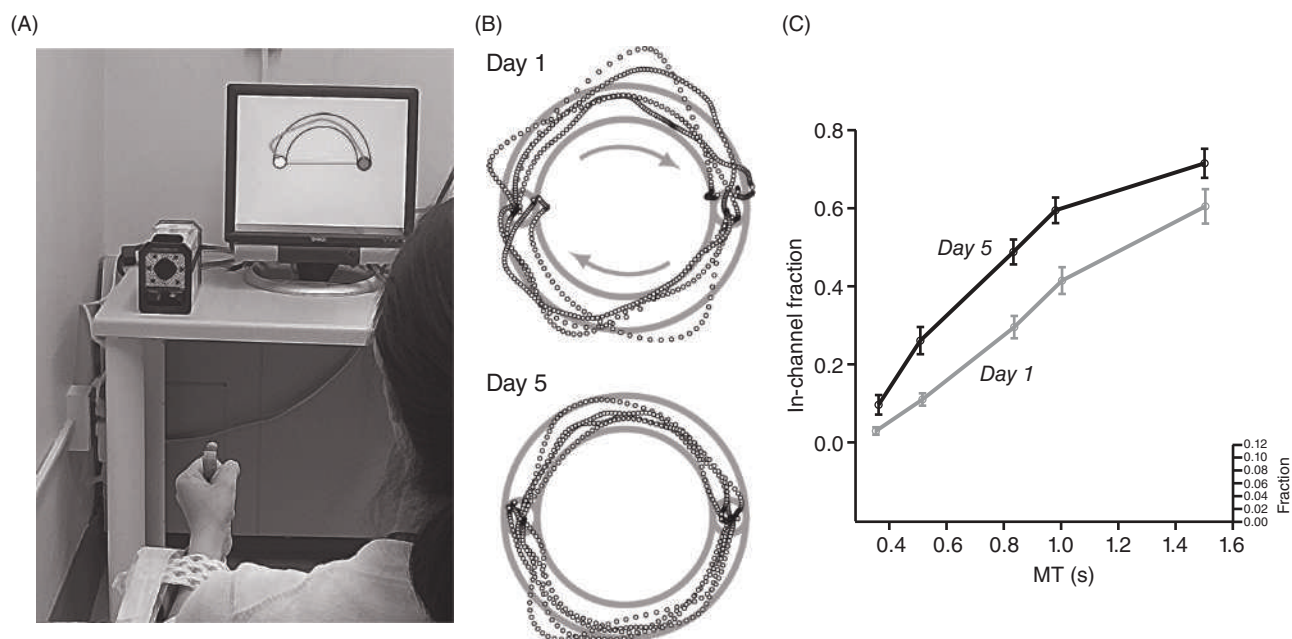


Figure 18 The arc-pointing task [adapted, with permission, from (398)]. (A) A picture of experimental setup: the participant controls a cursor on the screen via wrist flexion-extension and pronation-supination, and try to move the cursor in a clockwise direction through a circular channel. A proreflex infrared camera tracks pointing direction of a reflective marker the participant wears on her index finger proximal interphalangeal joint, projecting it as a cursor on the screen. (B) Representative trajectories before (day 1, top panel) and after (day 5, bottom panel) training. (C) Group-level performance before and after training. Proportion of within-channel movements as a function of movement time (MT). The histogram shows the distribution of average MT.

evidence for improved feedback control with practice, which likely contributed to the reduced movement variability. Both the presence of submovements and feedback control argue strongly against the idea that stereotypy was attributable to feedforward replay of motor commands. In a follow-up fMRI study, the same task was used to investigate neural correlates of improvements in motor acuity. Notably, learning-related activation changes, controlling for performance level, were found in the contralateral premotor and primary motor cortex and the ipsilateral cerebellum (399). Thus, as suspected, when learning was emphasized at the level of execution, changes *were* seen in contralateral motor cortical areas, just as has been described in animal models of motor skill learning.

The motor learning field does not yet possess an adequate computational model for practice-induced increases in motor acuity. The models discussed in other parts of this review instead speak to how an average movement is converged upon and properly selected. They do not address how execution of the selected action then improves with subsequent practice. We also do not know precisely which neural changes are responsible for increased motor acuity, either structurally or physiologically. As we have already discussed, neither expansions in cortical maps nor changes in spine density appear to be necessary for motor skill expression. It is not clear that just finding correlations between any kind of structural change in neural substrate and improved behavioral performance will lead to the kind of understanding we are looking for (248). Improvements in motor acuity that occur

with practice may be driven by increased signal-to-noise ratio in motor cortical representations (220) and better feedback control, as suggested by the evidence presented above. These cortical changes are perhaps aided by improved state estimation by forward models, possibly in the cerebellum (387). It has been proposed that unsupervised or statistical learning is the algorithm used by cortex (87). At this point, however, we cannot go much beyond informed conjectures about the kind of motor learning that most people associate with the word colloquially, that is, improvements in execution quality of a continuous motor skill.

Expertise

This review has focused on motor learning, and, arguably, the ultimate example of motor learning can be seen in elite sports, with athletes who have trained for years to maximize their performance. It is likely, however, that the bulk of the time required to become an expert in sport is actually dominated by improvement of its cognitive components, rather than by improved motor execution. This conclusion is supported by the fact that chess, sports, and music require similar amounts of deliberate practice to achieve expertise, even though there is obviously no sensorimotor skill component to chess. What these tasks do share, however, is the need to develop cognitive strategies. An expert tennis player analyzes the game of their opponent before and during the match and then comes up with a game plan that extends across games and sets.

Another likely reason that certain motor tasks take years to gain expertise in is the number of interacting factors that must be taken into account before any given movement is executed. For example, in tennis, stroke selection and body movement will vary depending on the court surface, wind conditions, humidity effects on the ball, and levels of sun and shadow. This complexity leads to a combinatorial explosion, akin to the possibilities in chess, resulting in a large, multidimensional space, and optimal actions must be found for *each* state in it.

It appears then that one can distinguish between two results of extended practice: better strategy development and action choice versus improved execution and more rapid selection of a chosen action. This distinction has also been described as the difference between executing a given strategy more quickly (skill) versus coming up with qualitatively different strategies (expertise) (40). Anders Ericsson (whose seminal work inspired the somewhat inaccurate, pop-journalistic “10,000 hours rule”), makes a similar distinction when he states: “With deliberate practice, however, the goal is not just to reach your potential but to build it, to make things possible that were not possible before (100).” This quantitative versus qualitative distinction is often reiterated but its importance to the neuroscience of motor learning is perhaps less appreciated.

The importance of cognition has been a recurring theme across almost all the varieties of motor learning we have discussed in this review, and thus it should not be surprising for it to also be important in expertise. In our view, the need to identify novel ways of solving the task, rather simply optimizing an existing approach, means that expertise, whether in motor or non-motor domains (e.g. chess or mathematics) is likely to depend critically on more general executive, memory, and cognitive control capacities. Therefore, cognitive processes should ultimately not be excluded from the definition of motor learning, but rather should be considered integral to our capacity for malleable and sophisticated movement skills.

Conclusion

In this review, we have attempted to survey the current experimental and theoretical landscape of motor learning. Our emphasis has been on characterizing the component behaviors that are probed by the tasks most frequently chosen by neuroscientists and psychologists in the field, namely those that fall into the categories of goal selection, action selection, and action execution (Fig. 1), with the term “motor learning” used in an inclusive sense in so much that we covered work that is consistently self-described as being about motor learning. The categories discussed (motor adaptation, sequence learning, *de novo* learning, and motor acuity) were primarily organized around the paradigms used to probe motor learning, however, it is likely that the underlying processes that support learning in these tasks in many cases overlap, likely because they modify common stages along the motor planning pathway.

Adaptation paradigms, for instance, can be viewed as posing a recalibration problem, and learning in adaptation tasks indeed seems to be partially supported by a cerebellum-dependent learning process that enables recalibration of movements. However, adaptation tasks can also be considered a kind of arbitrary visuomotor association—in reaching tasks, for instance, participants must learn to associate a different action with each possible target location. It is therefore unsurprising that many different learning processes also participate in helping to learn to counter the perturbation. Sequence tasks, like adaptation tasks, are also likely to be supported by multiple learning processes, although, unlike recalibration in adaptation tasks, sequence learning may not isolate any purely motoric phenomenon of interest. Instead, the notion of sequences, at least in the motoric sense, can perhaps be subsumed under the more basic components of skill: fast action selection and accurate execution of individual actions, which were covered in the sections on *de novo* learning and motor acuity, respectively.

In addition to adaptation and sequence learning, we have discussed *de novo* learning—the construction of new controllers, which become automatized through practice—and improving motor acuity—increasing the speed and precision of execution of a selected action. These forms of learning have been relatively less well studied, and their neural basis less well characterized. We suggest that approaches that emphasize these forms of learning will provide a better foundation for the study of motor skill learning.

Acknowledgements

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